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Translocation, Homing Behavior and Habitat Use of Groundfishes Associated with Oil Platforms in the East Santa Barbara Channel, California

Kim M. Anthony,[1] Milton S. Love,[2] and Christopher G. Lowe[1]

[1]*Dept. of Biological Sciences, California State University Long Beach, 1250 Bellflower Blvd., Long Beach, CA 90840, USA*
[2]*Marine Science Institute, University of California Santa Barbara, Santa Barbara, CA 93106*

Abstract.—All offshore oil and gas platforms have finite economic life spans. One of the decommissioning options for these platforms is complete removal, requiring the use of explosives to dislodge the support structure from below the seafloor. Off California, this decommissioning option would kill large numbers of platform-associated and commercially important groundfishes that inhabit the bases of the platforms, and may potentially affect regional fish populations. Capturing and translocating fishes before removing a platform might mitigate the effects of platform removal. In this study, we acoustically tagged 79 rockfishes and lingcod from three oil platforms in the east Santa Barbara Channel and translocated them to a natural reef inside a state marine reserve at Anacapa Island to determine whether individuals would home back to their platforms of capture, or take up residency at their new location. Movements between natural and platform habitats were monitored over a two-year period. Twenty-five percent of all tagged fishes translocated to a natural reef returned to their home platforms relatively quickly, traveling distances from 11 km to ≥18 km, in 10.5 h to 17 d. Those that did not home took up residency at Anacapa Island, moved to Santa Cruz Island or out of the range of detection. Although a small proportion of fish (25%) homed back to the platforms, a higher proportion (75%) remained at their platforms of release. Those that homed back to their platform of capture did so relatively quickly (avg 15 ± 31 d). Lingcod had the highest probability of homing back to their platform of capture, typically doing so in < 1 day. These results suggest that fish translocation may be a successful, but costly mitigation strategy for platforms that require full decommissioning and that some species may be more successfully translocated than others.

Introduction

In California, offshore oil platforms have accumulated a broad array of marine life from the surface to the seafloor in areas that are otherwise depauperate of natural reef or complex structure. Platforms in the Santa Barbara Channel have been found to function as *de facto* reserves protecting several species of groundfishes from fishing pressure that has resulted in their localized depletion on natural, unprotected reefs (Helvey 2002, Love et al. 2003). Until recently, all obsolete platforms off California required full decommissioning,

Corresponding author: Kim Anthony, kim.anthony@sce.com

resulting in the removal of the entire structure to 4.5 m below the seafloor and subsequent restoration of the seafloor to its original state (Schroeder and Love 2004). In the Gulf of Mexico, widespread support of coastal states led to a federal Rigs-to-Reefs program (Dauterive 2000), designed to support the sportfishing and recreational diving industries by creating a network of artificial reefs from the partial removal and toppling of obsolete oil platforms. Platform reefing in California has been a controversial issue, but a new State policy now allows for partial removal (California Marine Resources Legacy Act 2010). However, not all platforms will be considered for reefing under the new policy; the effects of the decommissioning process on marine life associated with those platforms need further evaluation.

Full removal of an obsolete platform will result in a complete loss of complex habitat and its associated marine community. While a majority of sessile organisms are lost as a result of full platform removal, mobile species have the capability to relocate during the decommissioning process. However, one method frequently utilized for full removal includes the use of explosives to sever the support structure below the seafloor (Schroeder and Love 2004), which results in large mortalities of fishes with swim bladders that reside around platforms (Bull and Kendall 1994). In this case, a majority of fish are killed before they have a chance to move away during the structure removal process. One potential mitigation option would be to translocate platform-associated fishes away from the platform prior to the implementation of explosives. However the success of translocation is dependent on the degree of site fidelity and movement of the species associated with the platform.

Platform surveys have shown that groundfishes observed around oil platforms are closely associated with the structure (Love et al. 2003). Typically, species like benthic rockfishes (*Sebastes* spp.) and lingcod (*Ophiodon elongatus*) that have a high affinity for complex substrata, also have small home ranges and exhibit high site fidelity (Matthews 1990ab, Starr et al. 2002, Lowe and Bray 2006). Lowe et al. (2009) found that some species of rockfish exhibited moderate to high degrees of site fidelity on offshore oil platforms with probable ontogenetic emigration. Therefore, translocation of residents could result in individuals "homing," defined as the ability to return to a home range after leaving or being displaced (Gerking 1959).

Despite a high degree of site fidelity, tagging studies have also demonstrated that rockfishes and lingcod are capable of moving significant distances over natural reefs and along coastlines. Previous displacement studies of rockfishes have indicated that they are capable of homing from 400 m to over 22 km (Matthews 1990ab, Pearcy 1992, Lea et al. 1999) and lingcod have been shown to home from distances of ~8 km (Lowe et al. 2009). Previous translocation experiments released tagged reef associated fishes over contiguous habitat, in relatively shallow depths and primarily along a coastline, all of which offer navigational aids to return. None have challenged homing ability by releasing fish in high-relief rockfish habitat or across distances and depths that exceed their known limits.

If full removal of some offshore platforms using explosives is to remain an option, translocating a proportion of the fish population to natural reefs as a mitigating alternative may be viable assuming a majority do not home back to the platform. Therefore, it is important to determine whether platform-associated groundfishes home after displacement. The goals of this study were to (1) determine whether platform-associated fishes would home back to resident oil platforms after being translocated to a natural reef, and (2) characterize patterns of movement on and between platform and natural reef habitats.

Methods

Study Site

The Santa Barbara Channel is bound on the south by the Northern Channel Islands (Anacapa, Santa Cruz, Santa Rosa, and San Miguel) and is approximately 100 km long and 50 km wide with seafloor depths exceeding 230 m mid channel (Fig. 1). Oil platforms Gail (225 m depth), Gilda (61 m), and Grace (91 m) are situated in the east Channel approximately 11 km, 17 km, and 18 km away from northeast Anacapa Island, respectively, and range from 5–8 km apart from each other. Most of the seafloor in the east Santa Barbara Channel consists of sand and mud habitat, so offshore oil platforms throughout this part of the Channel may constitute significant fish habitat.

Tagging

All fishing was conducted from an 8 m vessel, which allowed for close access to the platform structure. While fishing on and near the seafloor in depths ranging from 61 to 225 m, fishes were caught on conventional hook and line using baited circle hooks. Once landed, fishes were held in the vessel's live well in chilled (10° ± 2° C) seawater. The condition of all fishes was assessed upon landing. Most were afflicted with some form of barotrauma, or a combination of signs (e.g., distended abdomen, exophthalmia, air bubbles under skin, or stomach protruded through mouth). Fishes judged to be in good condition and with milder signs of barotrauma were held for tagging (Fig. 2). To minimize handling time and risk of puncturing vital organs, swim bladder venting with hypodermic needles was not performed—the surgical incision typically released an adequate amount of pressure. Fishes were surgically fitted with V13 R-code acoustic transmitters (model V13-1H-R04K, 156 dB power output, 13 mm diameter × 36 mm length; Vemco, Halifax, Nova Scotia, Canada), which were coated in a blend of paraffin and beeswax (2.3:1.0) to prevent immunorejection (Lowe et al. 2003). Transmitters emitted a 69 kHz pulse train pseudo-randomly in 150 to 300 s intervals, which allowed for a nominal battery life of ~4 yr. The pulse train contained information unique to the identification code for each transmitter. Prior to tagging surgery, fishes were anaesthetized in a cooler containing chilled seawater (~10° C) with 20 ppm clove oil and measured for total lengths (cm). A 1.5 cm incision was made approximately 1 cm from the ventral midline of the fish, between the pelvic fins and the anal vent through the peritoneum. A V13 transmitter was inserted into the abdominal cavity and the incision was closed with one or two interrupted dissolvable sutures (Ethicon Chromic Gut, Johnson & Johnson). An external identification tag was inserted into the dorsal musculature of each fish in the event that an individual was recaptured by an angler, or sighted during submersible surveys. Fishes were subsequently held on the vessel's chilled seawater live well for transport. Moribund fishes were euthanized and kept for other research purposes (Rogers et al. 2008), and live fishes too small for tagging were released to a depth of 35 m in an inverted, weighted milk crate (Jarvis and Lowe 2008) at the site of capture.

Acoustic Receiver Deployment

Automated omni-directional acoustic receivers (VR2, Vemco Ltd.) were deployed on each of the three oil platforms' north and south mooring buoys as described by Lowe et al. (2009). Due to security restrictions, VR2 receiver deployment was not possible at Platform Gilda until 20 October 2006, over 2 mo after the initial deployment of all other

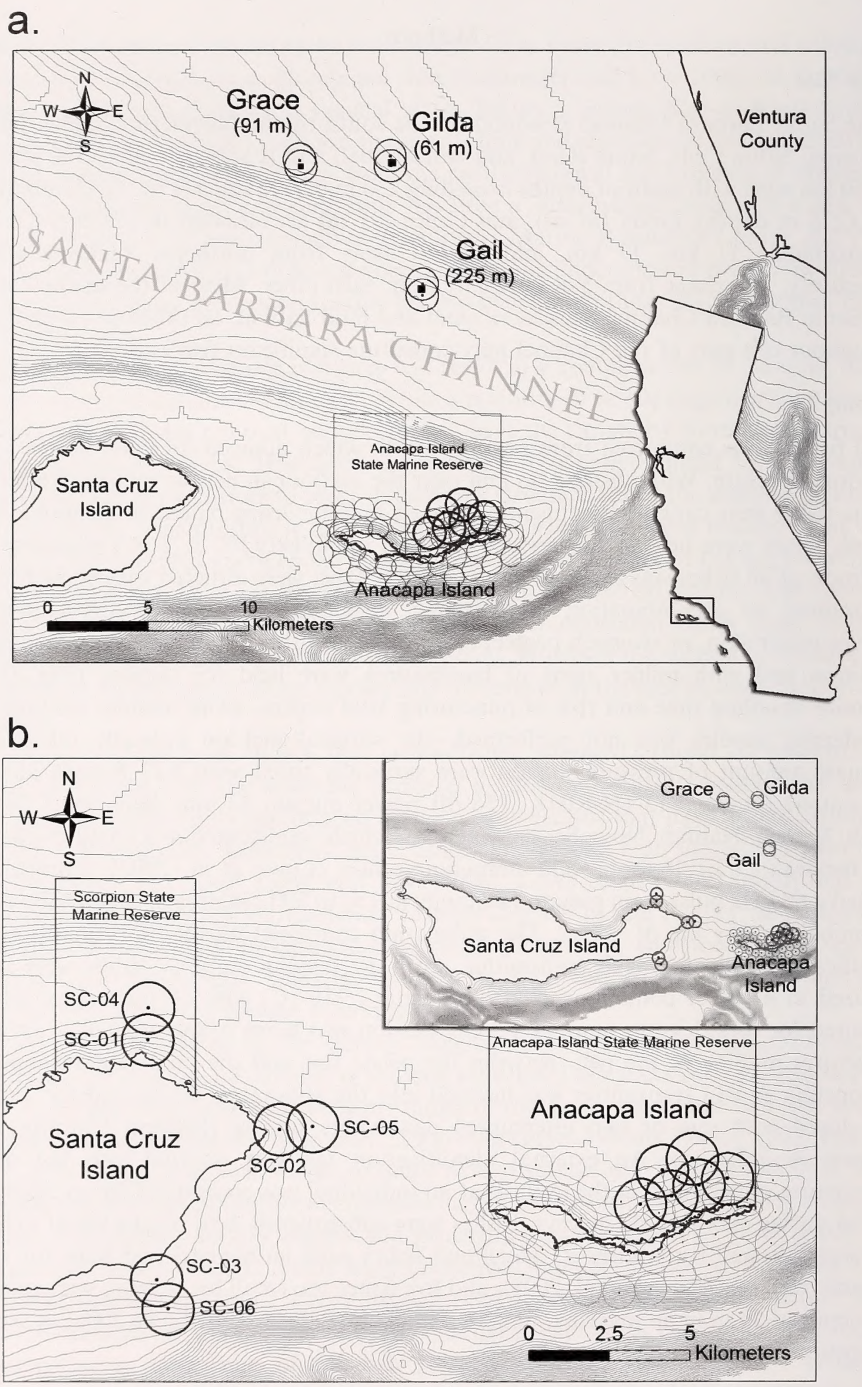

Fig. 1. Inset of panel (a) shows the study site offshore Ventura County, California in the Santa Barbara Channel. Panel (b) details the study site between the east end of Santa Cruz Island and Anacapa Island. Circles surrounding the dots at each oil platform and at Anacapa Island characterize 800 m detection zones around each VR2 receiver. Smaller, faded circles in a two-tiered array around Anacapa Island depict 500 m detection zones around VR2 receivers maintained by the Pfleger Institute for Environmental Research (PIER) through October 2006. Depth contours are 10 m.

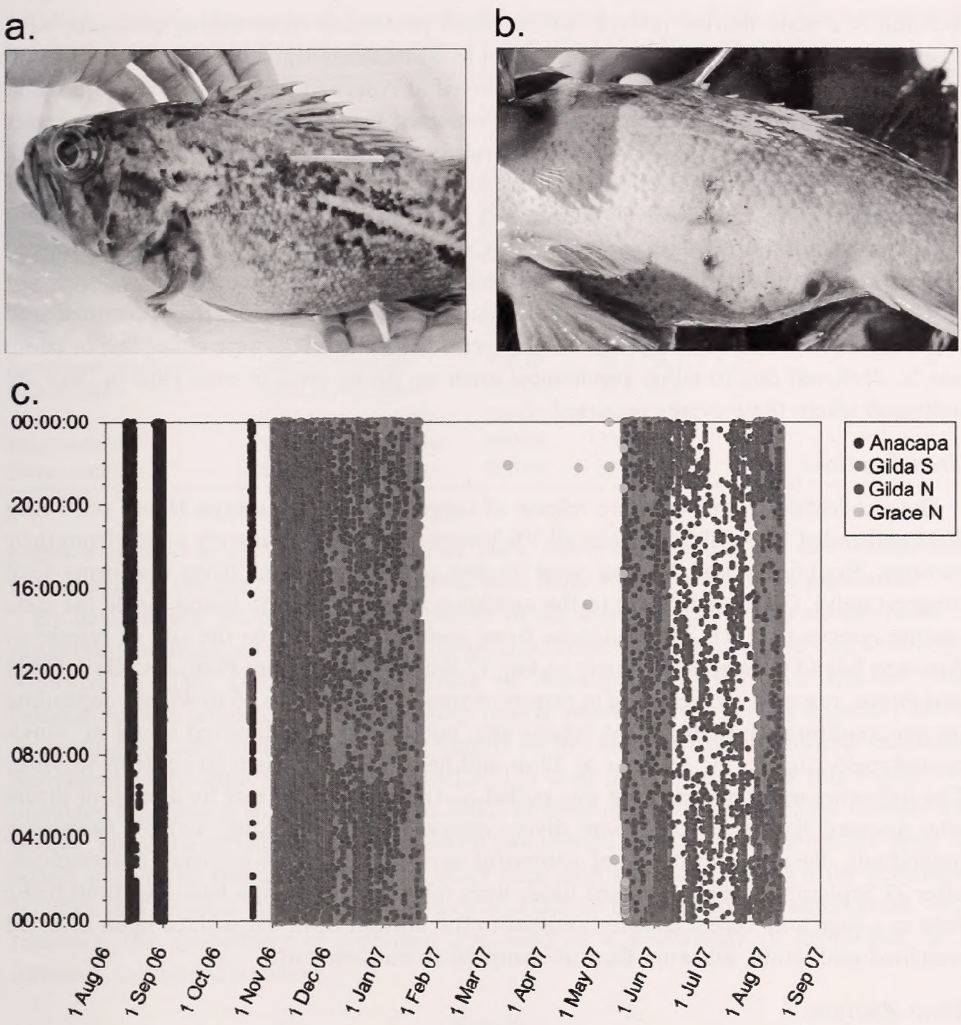

Fig. 2. Recaptured tagged vermilion rockfish showing (a) an external ID tag and (b) ventral view of a healed surgical incision. Panel (c) shows the date-time scatter plot of individual SMIN 3784, detected at Anacapa Island and subsequently at Platform Grace, where it was recaptured and translocated to Anacapa for a second time.

receivers. VR2 receivers were estimated to have a detection range of approximately 800 m, based on range tests performed with V13 transmitters before any fish was tagged and released. Two VR2 receivers deployed on the north and south sides of each platform provided a detection coverage area around the jacket of approximately 1 km^2. VR2 receivers recorded and stored the date and time of detection and the unique identification code of each fish if the transmitter emitted a signal inside the detection range. Previous studies at Platforms Gilda, Grace and on the San Pedro shelf have found no indication of diel ambient noise that would confound interpretation of diel activity/detection patterns (Lowe et al. 2009; C. Mireles Unpub. Data).

The northeast side of Anacapa Island was chosen as a natural reef site to translocate fishes because of its accessibility, its historically rich rockfish abundances and because the

location is a state marine reserve, which offers protection from fishing pressure. VR2 receivers were deployed at depths from 55 m to 80 m, comparable to two of the three oil platforms of study. Depths of receivers deployed at Anacapa Island exceeded safe scuba diving limits, therefore VR2 receivers were retrieved from depth using acoustic releases (AR-50 Sub Sea Sonics, San Diego). Once released from the sand bag anchor, the VR2 receiver-acoustic release unit floated to the surface for recovery. The Pfleger Institute of Environmental Research (PIER) maintained an array of VR2 acoustic receivers around Anacapa Island and the east end of Santa Cruz Island, which also detected any tagged fishes for this study that moved within detection range of those receivers.

VR2 receivers were retrieved and downloaded every 2 mo as weather permitted and rebatteried every 6 mo over the 620 d study period. Several VR2s were either lost or could not be deployed due to either mechanical error or strong swell events; gaps in data are indicated where these events occurred.

Translocations

Data collection began with the release of tagged fishes at Anacapa Island on 6 Aug 2006 and ended 12 April 2008 when all VR2 receivers were permanently pulled from their stations. Rockfishes and lingcod were tagged and translocated from Platforms Gail (lingcod only), Gilda and Grace to the northeast side of Anacapa Island inside the state marine reserve (Fig. 1). The distances from each oil platform to the site of release at Anacapa Island were approximately 11 km, 17 km and 18 km from Platforms Gail, Gilda and Grace, respectively, resulting in transport times ranging from 15 to 45 min depending on sea conditions. Initially at the release site, tagged fish were lowered in a 1 m^3 vinyl-coated mesh cage to the seafloor at 58 m and held there overnight to confirm survival. The following morning, the cage was pulled to 18 m depth and met by a team of divers who assessed the fishes' condition; divers released healthy-looking, actively swimming individuals. Based on evidence of successful survivorship following cage observations, after 23 September 2006, all tagged fishes were released at Anacapa Island without being held in a cage and were thereafter assisted to the bottom from the surface in an inverted weighted milk crate, allowing them to swim away on their own.

Data Analysis

Transmitter deployment (i.e., fish release) spanned two consecutive summers (2006–2007), thus data were standardized from the day each fish was released, defined as "days since released." A fish was considered present at any given location if it was detected on a receiver at least three times in one day within one hour. Based on those criteria, telemetry data were used to determine (1) whether fish homed, (2) the residence time at any given location, (3) transit times and (4) temporal patterns in detection. Emigration rates of tagged fishes in this study were characterized using a logarithmic equation (Lowe et al. 2009). Working from the same oil platforms as the current study, Lowe et al. (2009) tagged rockfishes and lingcod and released them onsite; the study served as a control and was used for comparison of emigration rates from the translocation site (Anacapa Island). Residence time was defined as the time an individual spent at its site of release before moving outside the range of detection. An individual was characterized as having taken up residency if it was detected at the same site consistently for at least 2 mos. The time elapsed from the site of release to an oil platform or other monitored location was considered transit time. Residence and transit times were compared among species. Differences in residence times of fishes at Anacapa Island were tested using a Mann-Whitney rank sum test. Two-sample

Table 1. Tagging summary of all fishes translocated from platforms Gail, Gilda, or Grace to a natural reef inside Anacapa Island State Marine Reserve. Total lengths (TL) were measured in cm.

Common Name	Species	Species Code	Size Range (TL in cm)	Platform (# of fish)		
				Gail	Gilda	Grace
Lingcod	*Ophiodon elongatus*	OELO	66.0–94.0	10	-	-
Mexican rockfish	*Sebastes macdonaldi*	SMAC	51.0	1	-	-
Greenblotched rockfish	*Sebastes rosenblatti*	SGBL	35.0	1	-	-
Brown rockfish	*Sebastes auriculatus*	SAUR	30.0, 37.0	-	2	-
Vermilion rockfish	*Sebastes miniatus*	SMIN	24.0–35.5	-	7	30
Copper rockfish	*Sebastes caurinus*	SCAU	25.5, 44.0	-	2	4
Widow rockfish	*Sebastes entomelas*	SENT	27.0–31.0	-	-	4
Squarespot rockfish	*Sebastes hopkinsi*	SHOP	28.2, 28.7	-	-	2
Blue rockfish	*Sebastes mystinus*	SMYS	27.0–34.0	-	-	5
Bocaccio	*Sebastes paucispinis*	SPAU	28.5–32.0	-	-	5
Flag rockfish	*Sebastes rubrivinctus*	SRUB	23.6–28.2	-	-	5
Starry rockfish	*Sebastes constellatus*	SCON	27.0	-	-	1

t-tests were used to (1) determine whether there was a difference in the size of fish that homed and (2) discern differences in transit time from Anacapa Island to platforms.

By determining the presence and absence of an individual on a day-to-day basis, a probability of detection was calculated for each combination of monitored locations (e.g., Anacapa to Gail, Gail to Grace, Grace to Anacapa, etc.) for each species. This calculation was adapted from probability matrix models developed by Gotelli (2001). According to Lowe et al. (2009) fishes tagged on the same offshore platforms exhibited movement away from the platforms within 175 d of their release. For this model, we predicted a period of movement within 200 d of their release over the 620 d monitoring period. Thus, the probabilities of movement (we termed these *probability matrix loops* to reflect movement amongst monitored sites) were calculated out to 200 d for vermilion rockfish and lingcod. Assuming the ability of a fish to be detected was equal at all VR2 receivers, the probability of detection was used as a probability of movement to a different monitored location.

Results

Acoustic data were analyzed for 79 individuals tagged and translocated from oil platforms Gail, Gilda and Grace to Anacapa Island (Table 1). A greater proportion of fishes did not home, but 25.3% of individuals (11 rockfishes, 9 lingcod) returned to the oil platforms of their original capture. Although one brown rockfish (*S. auriculatus*) homed back to Platform Gilda, statistical analyses focused on the vermilion rockfish and lingcod. One previously tagged vermilion rockfish (SMIN 3784, Table 2) was recaptured at Platform Gilda, but the time of arrival at the platform could not be determined due to the absence of VR2 receiver coverage there until the day it was recaptured on 20 Oct 2006 (Fig. 2ab). This fish displayed minor signs of barotrauma (slightly distended eyes and bloated abdomen) upon recapture, but appeared to be in good physical condition when taken back to Anacapa Island for a second time. Twelve days later on 2 Nov 2006, the same individual (SMIN 3784) arrived at Platform Gilda again until 23 Jan 2007. After a period of absence (nearly 4 mo), this fish was once again detected at Platform Grace until 16 May 2007 (Fig. 2c). It was last detected at Platform Grace on 16 May 2007 at 01:52 h and moved back to Platform Gilda at 05:00 h the same day.

Table 2. Summary of all fishes that homed after translocation from platforms Gail, Gilda, or Grace to Anacapa Island. Each species is represented by a shorthand code and unique ID number.

Common name (Genus species)	Platform	Code	TL (cm)
Lingcod	Gail	OELO 3704	84.0
(*Ophiodon elongatus*)		OELO 3719	82.0
N = 9 out of 10		OELO 3733	78.0
		OELO 3736	94.0
		OELO 3742	65.0
		OELO 3767	90.0
		OELO 3777	89.0
		OELO 3781	89.5
		OELO 3787	74.0
Brown rockfish	Gilda	SAUR 3783	37.0
(*Sebastes auriculatus*)			
N = 1 out of 2			
Vermilion rockfish	Grace	SMIN 3743	33.0
(*Sebastes miniatus*)		SMIN 3752	35.3
N = 10 out of 30		SMIN 3758	35.3
		SMIN 3768	34.0
		SMIN 3771	27.5
		SMIN 3784	29.0
		SMIN 3785	30.2
		SMIN 3790	32.0
		SMIN 3795	32.0
		SMIN 3797	33.8

Some catch and release mortality was expected from the time of release up to approximately 10 d (Lowe et al. 2009), as indicated by an initial sharp decline in the number of fishes detected at Anacapa Island; however, some of this decline was coupled with a concomitant increase in the number of fishes detected at the platforms (Fig. 3). Three VR2 receivers were lost at Anacapa Island between 22 Sep 06 and 20 Dec 06, but immediately after they were replaced (20 Dec 06, near day 145), the number of fishes detected increased. The initial rapid decline in the number of fishes detected during the first 15 d since release (−3.50 fish/d) was attributed to mortality and/or immediate emigration from Anacapa Island. By the time the last individual homed (47 d), emigration rates slowed to −0.193 fish/d until 55 d, then stabilized to −0.026 fish/d from 140 d through the end of the study. A logarithmic equation best described the decrease in the number of fishes detected at Anacapa Island over the course of the study period (Fig. 3) ($y = -5.1964\ln(x) + 38.118$; $R^2 = 0.6278$).

Straight line distances from the site of release at Anacapa Island to each of the three platforms were the assumed minimum distance homing routes (Fig. 4). Lingcod traveled a minimum distance of 11 km back to Platform Gail, vermilion rockfish moved 18 km to Grace, and one brown rockfish moved 17 km to Gilda. One vermilion rockfish (SMIN 3795) was detected at Platform Gail before returning to Grace, increasing its homing distance by 1 km (19 km total).

All fishes that homed did so in a mean (± SD) of 14.7 ± 30.6 d after their release, and their residence times ranged from <1 to 47 d (Fig. 5a). Lingcod spent significantly less time at Anacapa Island before homing than did vermilion rockfish ($W = 55.0$, $p = 0.005$, $df = 17$). Lingcod had the shortest mean transit time (1.4 ± 1.22 d) with the fastest

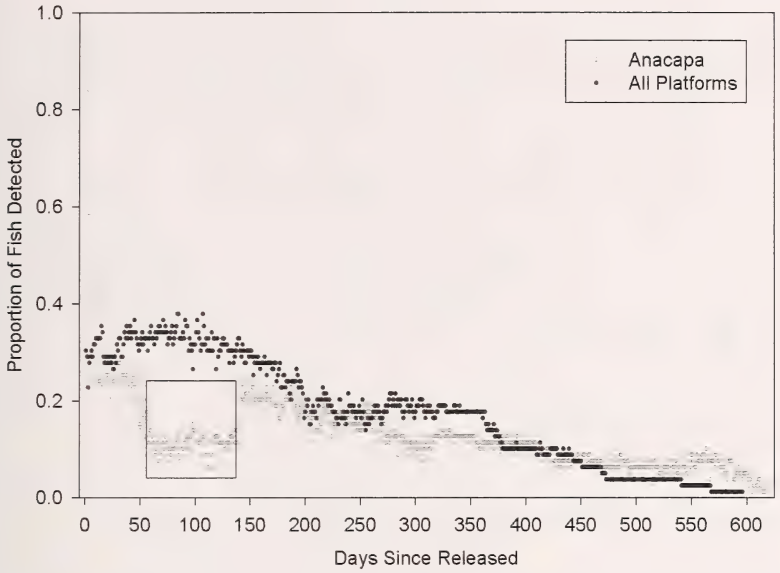

Fig. 3. Proportion of tagged rockfishes and lingcod detected inside the VR2 acoustic array at Anacapa Island (gray dots) and at all three oil platforms (black dots) each day since fishes were released. The black box surrounds detections spanning 88 d where three VR2 receivers were lost at Anacapa Island.

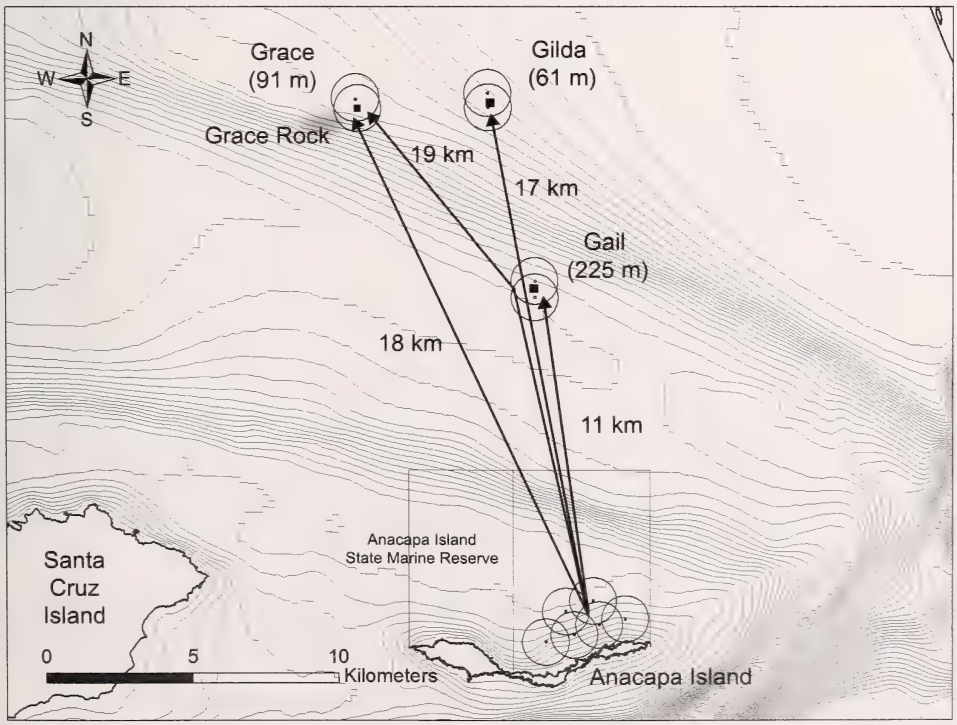

Fig. 4. Map showing minimum distance travel routes (in km) for individuals that homed after translocation. Depths of each platform are indicated in parentheses. Depth contours are in 10 m increments. Circles indicate 800 m detection zones around each of 12 stationary VR2 receivers (black dot).

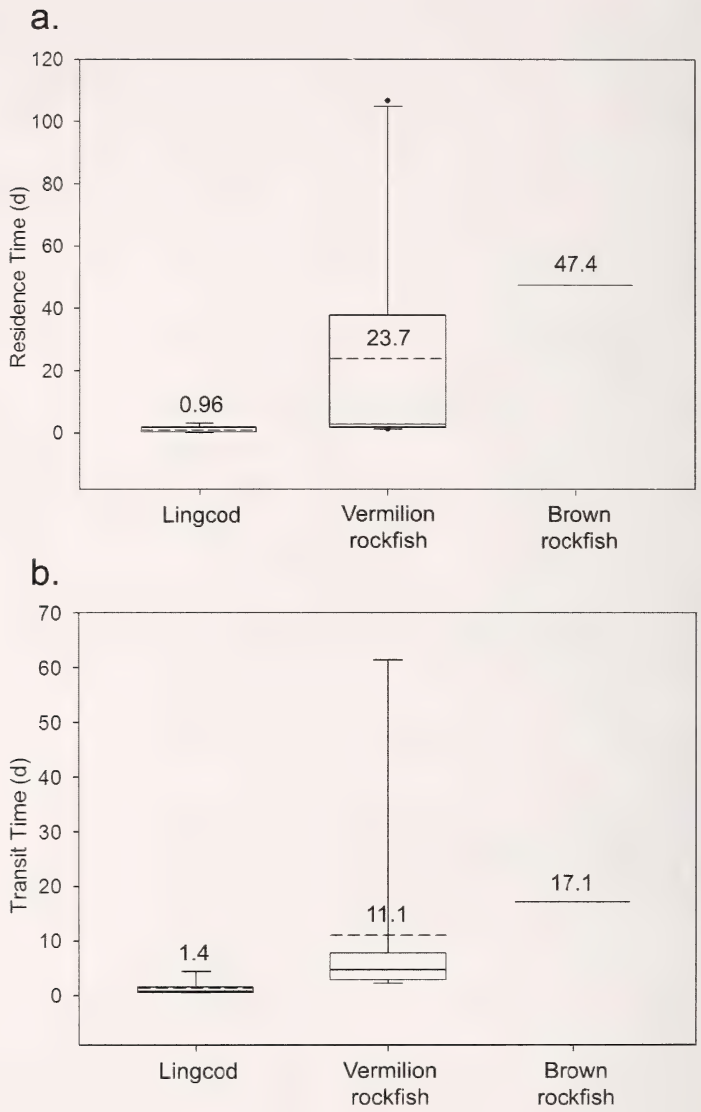

Fig. 5. Box plots of (a) presence times (in days) and (b) transit times for lingcod, vermilion rockfish, and one brown rockfish that homed back to their oil platforms of capture. Values shown are means, which are also indicated by the dotted line, except for the brown rockfish, for which only one individual homed. Upper and lower hinges represent 75th and 25th percentiles, respectively, while the median is shown as a solid line inside the box (visible only for vermilion rockfish). Vertical bars show the minimum and maximum values with outliers indicated by black dots.

individual homing 11 km in 10.5 h (Fig. 5b). Rockfish that homed were larger (32.6 ± 2.88 cm TL (± SD)) compared to those that did not (30.2 ± 4.32 cm TL) (p = 0.04, df = 67, t = 1.8).

Movement patterns were idiosyncratic and no one pattern was attributable to a given species. Some individuals exhibited diel patterns in movement upon return to the platforms, e.g., vermilion rockfish SMIN 3771 was detected on both north- and south-stationed VR2 receivers, showing a higher concentration of detections between 06:00 h

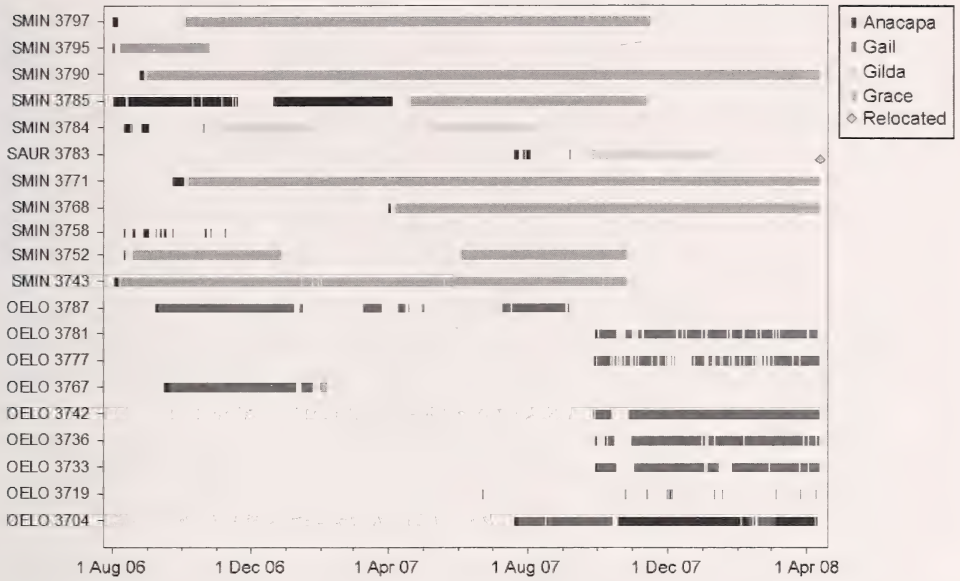

Fig. 6. Daily detection plot of all fish that homed: vermilion rockfish (SMIN), brown rockfish (SAUR), and lingcod (OELO). For each individual along the y-axis, a shaded mark exists for each date (x-axis) it was detected at Anacapa, Platforms Gail, Gilda or Grace. The gray diamond on the last day of SAUR 3783 indicates that the fish was relocated during mobile acoustic surveys with the VR100, after months of remaining undetected by the stationary VR2 receivers. Vermilion SMIN 3784 homed to Platform Gilda and was subsequently recaptured in Oct. 2006. It was taken to Anacapa Island for a second time and homed again, back to Platform Gilda.

and 19:00 h on the south side of Platform Grace. One vermilion rockfish and three lingcod exhibited movement between platforms after returning to their home platforms (Fig. 6). Two vermilion rockfish (SMINs 3795 and 3790) were detected at Platform Gail before homing to Platform Grace, traveling at least 19 km. SMIN 3784 (Fig. 3) homed to Platform Gilda from Anacapa Island twice, moved to Platform Grace then back to Platform Gilda, traveling a total distance of 27 km. Lingcods OELO 3787 and OELO 3777 homed from Anacapa Island to Platform Gail, moved to Platform Grace and subsequently returned to Platform Gail, each moving a minimum of 27 km. OELO 3767 traveled 35 km, having homed to Platform Gail, moved to Platform Grace and returned to Platform Gail, but moved to Platform Grace 14 d before going undetected. After homing to Platform Gail, OELO 3704 moved back to Anacapa Island for nearly 4 mo before returning to Platform Gail for 21 d, then moved back to Anacapa Island, traveling a distance of at least 44 km. From early March 2008 through the remainder of the study, this lingcod was detected at Anacapa Island.

Non-homing fishes

Fifty-nine individuals did not home and were either detected within the Anacapa Island VR2 receiver array or moved out of the range of detection for some portion or during most of the 620 d monitoring period. Fishes that did not home included bocaccio (*S. paucispinis*), Mexican rockfish (*S. macdonaldi*), greenblotched (*S. rosenblatti*), starry (*S. constellatus*), copper (*S. caurinus*), brown (*S. auriculatus*), squarespot (*S. hopkinsi*), widow (*S. entomelas*), blue (*S. mystinus*), flag (*S. rubrivinctus*), 27 vermilion rockfish and one

lingcod. While many individuals went undetected after variable amounts of time after release (days to months), 12 individuals continued to be detected very close to, or through the end of the study period, indicative of residency.

Two examples of fishes that appeared to take up residency within the Anacapa Island VR2 array were a flag rockfish (SRUB 3734) and a bocaccio (SPAU 3760); they showed clear movements based on their detections between at least two VR2 receivers. Flag rockfish SRUB 3734 revealed considerable movement between several VR2 receivers, including those of PIER. Shortly after their release at Anacapa Island, a flag (SRUB 3746, 25.0 cm TL), a blue (SMYS 3748, 32.7 cm), and a vermilion (SMIN 3751, 29.5 cm) rockfish moved to Santa Cruz Island, where they were detected by VR2 receivers maintained by PIER. These three fish remained at Anacapa Island from 2–7 d before they moved out of the range of detection and were subsequently detected at PIER receivers SC-01 and SC-04 inside the Scorpion State Marine Reserve (Fig. 1b). Although four additional VR2 receivers were deployed around the east end of Santa Cruz Island, no individuals were detected at those locations. VR2 receivers were removed by PIER in Oct. 2006, therefore it was impossible to know if any fishes thereafter moved to Santa Cruz Island.

Vermilion rockfish that homed exhibited seven patterns of behavior, all starting at Anacapa and moving (1) to Grace, (2) to Gilda, (3) to Gail, (4) from Grace to Anacapa, (5) remaining at Anacapa, (6) remaining at Gilda and (7) remaining at Grace (Fig. 7a). Vermilion rockfish caught from Platform Grace were most likely to stay there if they returned (64.5% probability). Alternatively, fish that were translocated to Anacapa Island had a 26.3% probability of staying inside the acoustic receiver array there. The third site most frequently visited by vermilion rockfish was Platform Gilda, where the probability of fish remaining there was 12%. Ten of 37 (27%) vermilion rockfish successfully homed, of which 40% (n = 4 of 10) visited Platforms Gail, Gilda or Anacapa Island before returning to Platform Grace.

Lingcod moved to either Anacapa Island or Platform Gail (Fig. 7b), regardless of where they were detected previously. Lingcod had the highest probability of being detected at Platform Gail (77.3%), or Anacapa Island (22.3%). To a much lesser extent, fish moved to Anacapa Island or Platform Gail from all other locations ($\leq$1.18%).

Discussion

The ability to return to a home range after displacement, or homing, is a well-documented phenomenon in fishes (Carlson and Haight 1972; Hallacher 1984; Markevich 1988; Matthews 1990ab; Pearcy 1992; Hartney 1996; Lea et al. 1999; Marnane 2000; Kaunda-Arara and Rose 2004; Starr et al. 2004). One of the earliest reports of homing in rockfishes was described by Carlson and Haight (1972), who displaced yellowtail rockfish (*Sebastes flavidus*) off southeast Alaska from their site of capture and reported tagged individuals that had homed back, including one individual that returned from 22.5 km. With the exception of Carlson and Haight (1972), previous displacement studies have tested homing ability within contiguous habitat or along a depth contour, thus providing a habitat boundary to follow. Fishes in the current study were translocated from their sites of capture offshore across a channel basin (>200 m depth). Despite these potential physical barriers, lingcod, vermilion rockfish and one brown rockfish successfully homed back to their platforms of capture, but also exhibited movement around, away from and between platforms after homing events.

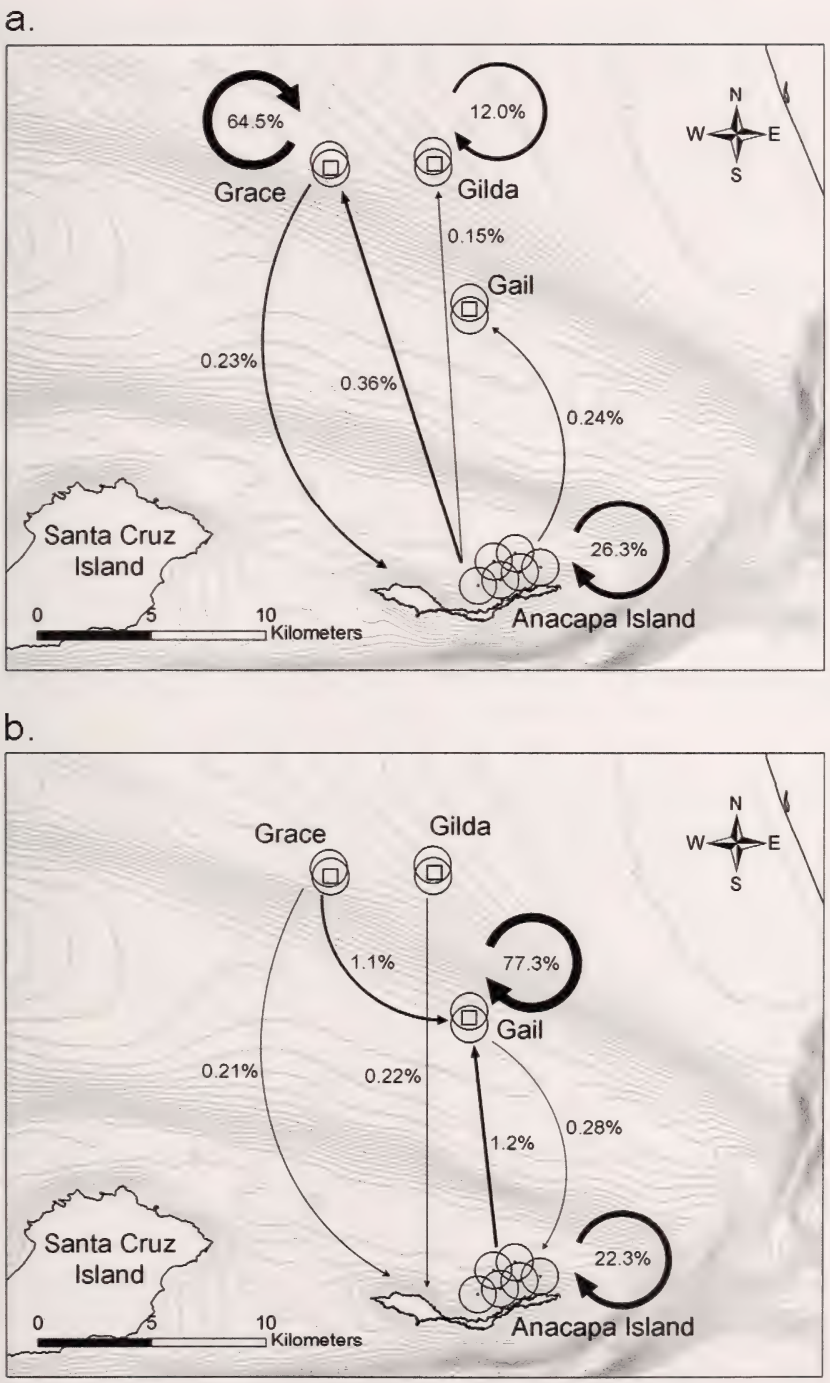

Fig. 7. Probability matrix loops for (a) vermilion rockfish and (b) lingcod movement overlayed on a GIS map for each site monitored during the study period. Probabilities of movements were calculated over a 200 d period. Thicker lines emphasize increased probability of movement in the direction of the arrow.

Tagged rockfishes and lingcod removed from offshore oil platforms and translocated to natural habitat at Anacapa Island exhibited the ability to home across previously unrecorded distances and in a relatively short time periods to their platforms of capture. Following release at Anacapa Island, the proportion of tagged fishes detected rapidly declined in the first 10 d, reflecting a departure from the receiver array coupled with some probable post-release mortality. Because detections at all three oil platforms subsequently increased, some of the immediate decline in detections of tagged fish at Anacapa Island during the first 50 d represents individuals that homed back to the platforms. Furthermore, a decrease in the proportion of fishes detected after 50 d was compounded by the temporary loss of three VR2 receivers at Anacapa Island. Although there was a steady decline in the number of fishes throughout the study period, the proportion detected at both Anacapa Island and the platforms fluctuated daily, indicative of individuals moving in and out of the receiver array, or around habitat that may have occluded signal transmission.

Lowe et al. (2009) observed a similar rate of emigration after releasing tagged rockfishes and lingcod at their platforms of capture. Ten days after their release, there was a rapid decrease in the number of fishes detected, followed by a slower decline through the duration of the study. We attributed the slow decline to emigration, as fishes moved from one platform to another, or away from areas of detection. Lowe et al. (2009) suggested that, over time, rockfishes likely emigrated away from platforms to other unmonitored locations, which may partially explain the disappearance of individuals in the current study.

Homing

The seafloor topography between Anacapa Island and Platforms Gail, Gilda, and Grace is largely a stretch of soft sediment with depths exceeding 230 m, presenting a large expanse of open water over relatively small patches of hard substratum. Notably, the homing distances observed in this study are the farthest reported for lingcod, vermilion and brown rockfishes. It is not known whether these fishes swam along the seafloor while homing or whether they traveled midwater or near the surface. Nevertheless, traversing these distances poses a greater challenge and risk, especially for relatively small fish, when crossing deep open water, than when following habitat along a coastline.

With the exception of one individual, all vermilion and the brown rockfish that homed were likely mature (range 27.5–35.3 cm TL). Vermilion rockfish mature as early around 31 cm (~ 4 yr), while 50% of brown rockfish are mature between 24 and 31 cm (~ 4–5 yr) (Love et al. 2002). Smaller, younger fish tend to occupy larger areas than adults that have established home ranges or territories (Larson 1980a; Lowe and Bray 2006) and are therefore expected to move more. In addition, they typically make ontogenetic shifts to deeper water as they mature (Love et al. 1991; Lowe et al. 2009), but not necessarily across long stretches of open water. However, smaller individuals that were translocated in this study tended not to home, and instead took up residency at Anacapa Island, or were not detected. Results indicate that among adults, individuals have variable propensities to home, while subadults showed a much lower probability of homing. Younger individuals may not develop an ability to home until they grow larger (Mathews and Barker 1983), or predation risk may be too high for subadults to leave a suitable, complex habitat offered by Anacapa Island. As they mature, fish may require additional resources that may compel them to shift their home ranges (Lowe and Bray 2006). For example, temporarily leaving a home range or territory to increase frequency or

probability of social interactions, such as spawning (Topping et al. 2006; Mason 2008), and being able to return is important for the success of some populations.

All fish that homed did so relatively quickly, leaving Anacapa Island after an average of 14.7 d following their release and taking from less than 24 h to travel back to the platforms. Compared to previous experiments displacing rockfishes, results from the current study revealed not only how quickly lingcod and rockfish can recover from catch, release, and tagging stress, but also the speed at which they orient themselves to a new environment and navigate home. Matthews (1990a) actively tracked copper and quillback (*S. maliger*) rockfish after displacing them 500 m from their home site and found that these species also homed quickly after release—after just 1–5 d. After translocation, short presence times at the site of release may be explained by a strong proclivity to home, or competition with resident fishes. Because of the protection offered inside the marine reserve, rockfishes at the site of translocation at Anacapa Island were not subjected to fishing mortality, which may have otherwise provided available space for new residents. This area of reef may have had well-established residents with territories, which could influence establishment of new colonizers (Larson 1980b) or it is possible that translocated individuals were able to assess the habitat quality simply preferred platform habitat over the natural habitat available. It is also possible that more individuals attempted to home, but either could not successfully navigate back to their platform, found more suitable habitat (unmonitored), or died trying to return.

The time of day and season during which homing occurred varied, but the departure time from the platforms after fish homed may have coincided with reproductive periods. Five vermilion rockfish (all adults) left Platform Grace between 25 Oct. and 16 Nov., and one lingcod left Platform Gail on 6 Feb. Although it was not known where these fish may have moved, all departed during a time that correlates with spawning season for these species (Love et al. 2002). Lowe et al. (2009) recorded an adult lingcod departing from Platform Gail and arriving in shallow water (~ 20 m) at Santa Cruz Island (9 km away) in mid-January. The same individual was detected again at Platform Gail only two days later. It was hypothesized that this was a female moving into a shallow reef to spawn, as this is a characteristic behavior for females of this species (Love 1996). Typically, adults that leave for spawning return to their home ranges. If their departure from the platforms was for spawning, then the five vermilion rockfish and one lingcod in this study should have been detected again by March or April. The absence of detections (presumably a failure to return) at the platforms may indicate that they left for purposes other than spawning, moved to different locations after spawning, or died trying to return.

Non-homing fishes

Two rockfishes (bocaccio, SPAU 3772 and widow rockfish, SENT 3753) that left Anacapa Island were detected for short periods of time at Platform Gail before apparently traversing back to Anacapa Island and subsequently falling out of detection altogether. This behavior may be representative of fish that left Anacapa Island to home, but were either unsuccessful, or moved to other unmonitored areas. Although they did not home, this bocaccio and widow rockfish were able to navigate between natural and platform habitat, a distance covering at least 22 km over open water. Homing has not previously been reported for bocaccio or widow rockfishes, but Hartmann (1987) reported long-distance movements of juvenile bocaccio (recaptured up to 148 km away) tagged from an oil platform in the north Santa Barbara Channel. Bocaccio are capable of long-distance movements and may even be able to home, but did not exhibit this behavior

in the current study. Hartmann (1987) also tagged widow rockfish, but none were recaptured away from their tagging sites, which would imply that this species exhibits strong site fidelity. Lowe et al. (2009) also found that widow rockfish have high site fidelity to offshore platforms.

Movements between platforms and Anacapa Island

It is not clear why lingcod and vermilion rockfish make such large migrations between platforms and natural habitat. Fishes may be forced to leave their home ranges for periods of time due to changes in water conditions, food resources, spawning, competition, or habitat quality, among other factors (Lowe and Bray 2006). Home range sizes were not quantified in this study, but movements of vermilion rockfish and lingcod away from home platforms with subsequent returns indicates that platforms may be important components of their habitat.

While it is not always clear what compels fish to move when they do, a behavioral response such as homing may confer a fitness advantage for a species. The movement of fish between platforms, and between natural habitat and platforms suggests that the risks associated with leaving protective habitat (e.g. predation, disorientation, loss of habitat) and traversing great distances outweigh the benefits of staying. Alternatively, the frequency of homing events might also indicate that the risks of leaving are low. Variation in temporal and spatial patterns of homing, movements and area use within and among species in this study illustrates behavioral plasticity present in adult rockfish and lingcod populations around offshore oil platforms; this, among other factors, may reduce competition and contribute to population stabilization.

Management

While this movement behavior has not previously been quantified, its implications for offshore oil platform decommissioning in California should be taken in consideration. Based on the longer-term patterns in detection after release, rockfishes and lingcod could indeed, be successfully translocated. While it may work better for some species (e.g. widow, squarespot, blue rockfishes) than others (e.g., lingcod, vermilion, and brown rockfishes) the success of a large-scale translocation would depend on a multitude of biological and logistical factors, such as the size of individuals, condition and care in handling of the fish, timing of platform removal and financial costs. Because a proportion of fishes (25% overall) homed back to platforms and did so quickly after release (23 d), translocation for individuals with inclinations to home would reduce the conservation benefits. Nonetheless, the greater proportion of fishes that did not home back to platforms would potentially be salvaged from the impacts of platform removal. Concurrently, translocation as a mitigation option could provide other biological benefits, such as reseeding depleted groundfish habitats, while rebuilding natural stocks.

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Environmental Impact Assessment: Detecting Changes in Fish Community Structure in Response to Disturbance with an Asymmetric Multivariate BACI Sampling Design

Christopher J.B. Martin, Bengt J. Allen, and Christopher G. Lowe

Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Blvd., Long Beach, CA 90840, USA

Abstract.—One of the primary challenges to detecting anthropogenic environmental impacts is the high degree of spatial and temporal variability inherent in natural systems. Planned or routine events that result in disturbance to populations and communities provide an opportunity for scientists to apply well-replicated and statistically powerful sampling designs to assess subsequent biological effects. For example, a thick layer of sessile invertebrates is the prominent biotic feature of intertidal and shallow subtidal portions of offshore petroleum platforms in southern California. Given the central role of such invertebrates in providing food and shelter, their presence can reasonably be expected to influence associated fish community structure. At one platform on the San Pedro Shelf, invertebrate biomass was completely removed from support pilings and horizontal crossmembers to a depth of 20 m with high-pressure water during a standard "hydrocleaning" event in November 2007. Three nearby platforms remained undisturbed, providing a unique opportunity to test for disturbance-related changes in the local fish assemblage and the overall time course of community recovery. The potential impact of the abrupt and intense removal of the invertebrate layer was assessed with survey data collected periodically for one year prior- and one year post-hydrocleaning in a modified Before-After-Control-Impact (BACI) design. Asymmetrical multivariate analyses of variance revealed a significant effect of disturbance to fish, driven largely by reductions in the abundance of numerically dominant blacksmith (*Chromis punctipinnis*). Nevertheless, the system was surprisingly resilient, recovering to pre-disturbance conditions within ten months. Our results demonstrate that a well-replicated BACI sampling design can detect even subtle biological changes in response to disturbance, a key step towards developing a mechanistic understanding of community disassembly in the face of increasingly frequent and intense perturbations.

Introduction

Natural and anthropogenic perturbations are a major driver of current and anticipated changes in population dynamics, species interactions, and community structure from local to global scales (Paine et al. 1998; Chapin et al. 2000). Resulting changes in biodiversity have the potential to significantly alter important ecosystem properties such as productivity, nutrient cycling and resistance to disturbance or invasion (references in Hooper et al. 2005). As a consequence, understanding the potential ecological effects of such changes has been the focus of intense theoretical and empirical research effort in

Corresponding author: Chris.Lowe@csulb.edu

recent years. Environmental variability is currently increasing in many parts of the world and ecological communities are experiencing associated increases in the intensity, frequency and scale of disturbance events (Easterling et al. 2000). Predicting how natural communities will likely respond to higher levels of disturbance has therefore been recognized as a critical research priority (Benedetti-Cecchi 2003; Boyce et al. 2006).

One of the primary challenges to detecting natural and anthropogenic environmental impacts is the high degree of temporal and spatial variability inherent in natural populations and communities. Many current sampling designs are based on Green's (1979) Before-After-Control-Impact (BACI) design. Replicated samples are taken before and after a putative environmental disturbance at both a control and the impact site. Evidence of a disturbance would be found as a statistically significant interaction between the differences in sample means in the two locations before versus after the disturbance (reviewed by Underwood 1993; 1994). Although widely used, conclusions drawn from such analyses do not provide a strong test for the presence of an impact, given their lack of spatial replication (i.e., there is only a single control and impact location). A more logical approach is to compare a potentially impacted site to multiple control locations; the existence of an impact can then be tested with asymmetrical analyses of variance (Underwood 1993; 1994). A disturbance that causes more change at the impact location than at the control locations will be detected as a different pattern of statistical interaction among sites before versus after the event, rather than as a main effect. This approach is both logically sound and statistically powerful, however, difficulty in predicting where or when a disturbance might take place means that the amount of pre-disturbance sampling is quite limited in most cases. Planned or routine disturbance events associated with human activities can provide an important opportunity to investigate the effects of disturbance on natural populations and communities with well-replicated BACI sampling designs.

In southern California, the intertidal and shallow subtidal portions of offshore petroleum platforms are blanketed by a variety of sessile invertebrates that includes bryozoans, sponges, tunicates, barnacles, and bivalves, particularly mussels (*Mytilus* spp.) and rock scallops (Bram et al. 2005). Held together by a web of byssal threads produced primarily by the mussels, the invertebrate layer can accumulate to thicknesses of greater than 30 cm (Continental Shelf Associates, Inc. 2005). The presence of this thick layer adds structural complexity to the otherwise smooth steel surface by providing three-dimensional habitat; such increases in local rugosity particularly benefit smaller mobile invertebrates and reef-associated fishes (Suchanek 1979; Friedlander and Parrish 1998; Lingo and Szedlmayer 2006). Mussels are the dominant competitor for primary space on hard substratum and support a diverse community of small invertebrates within the bed that are prey for abundant microcarnivorous fish that represent a key intermediate link in coastal marine food webs (Seed and Suchanek 1992; Page et al. 2007). Mussels also provide strong benthic-pelagic coupling, moving large amounts of energy from the water column to the benthos and are themselves a key source of food for various fishes, seastars, whelks, and crabs (Paine 1966; Wootton 1994).

The sessile invertebrate layer encrusting the submerged support pilings and horizontal cross-members of petroleum platforms can rapidly become extremely dense and heavy due to elevated growth rates resulting from constant immersion (Page 1986). High offshore primary production (e.g., high phytoplankton concentration) typically enhances food supply to filter-feeders, leading to higher survival, growth rates and reproductive output (Menge et al. 1997). Mussels held on moorings offshore from intertidal sites grow

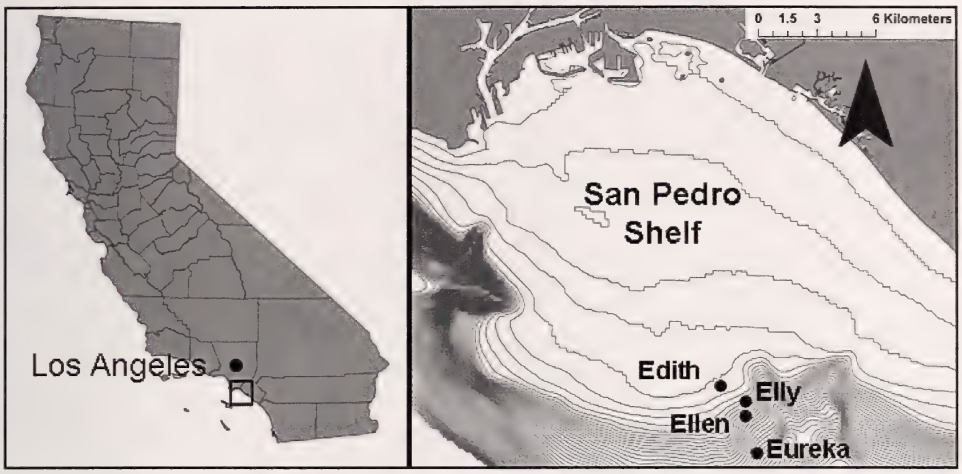

Fig. 1. A bathymetry map of the San Pedro Shelf, southern California, USA, and the locations of the four offshore petroleum platforms surveyed in this study. Isobaths are in 10-m increments. Map created by C. Mireles (CSULB).

at much higher rates than those in the corresponding intertidal areas (Blanchette et al. 2007). On offshore petroleum platforms, the resulting high biomass levels create a safety concern for normal operations (G. Shackell, U.S. Minerals Management Service, pers. comm.), such that federal law requires the periodic removal of the invertebrate layer in order to maintain structural integrity of the platforms. The regular nature of this particular event presents a unique opportunity to investigate the potential effects of disturbance on a biological system.

The mid-water fish assemblages of petroleum platforms on the San Pedro Shelf are largely comprised of nearshore reef-associated species (Martin and Lowe 2010). As many of these species are typically dependent upon natural rocky reef habitats for shelter and prey, the dense invertebrate layer on these platforms presumably provides these resources in a location where they would otherwise not be found (Stephens et al. 2006). As a consequence, any changes in the abundance and distribution of *Mytilus* spp. on petroleum platforms will likely result in widespread and significant alterations to the species identity and relative abundances of platform-associated fish (e.g., Syms and Jones 2000). Here we use a spatially- and temporally-replicated BACI framework to document the effects of a hydrocleaning event on the associated mid-water fish community of a southern California petroleum platform, relative to multiple control locations. As there was only one hypothesized "impact" platform versus three "control" platforms, this is an asymmetrical design (Underwood 1993, 1994).

Methods

Fish abundance surveys

Bi-monthly mid-water fish surveys were conducted at four offshore petroleum platforms on the San Pedro Shelf between November 2006 and September 2008. All surveyed platforms (Edith, Ellen, Elly, and Eureka) were within a four-km^2 area in water depths ranging from 49 to 212 m (Fig. 1). Because of their close proximity to one another, surface water conditions (e.g., wave exposure, temperature, light, pH, and chlorophyll *a*) were similar among the four platforms (Martin 2009). In November 2007,

a routine hydrocleaning operation was conducted at platform Elly; this event removed most of the encrusting invertebrate layer to a depth of 20 m, converting species-rich spatially-heterogeneous biogenic habitat to species-poor spatially-homogeneous steel support beams. In contrast, the three other platforms remained undisturbed. All four platforms were surveyed seven times both before and after the hydrocleaning operation.

Methods used to survey fish assemblages at the SPS platforms were replicated from those used by Love et al. (2003). SCUBA divers identified, tallied, and estimated the length of all the fish encountered within a designated window along a volumetric belt transect (2 m $\times$ 2 m, except along the outside perimeter where the window was 6 m wide $\times$ 2 m high to potentially include platform-associated species in the nearby water column). One diver tallied and identified all fishes to the lowest possible taxonomic level and estimated fish total lengths into 5-cm intervals. A second diver followed while operating an underwater digital video camera. Video footage was used to calibrate fish identification and assess inter-observer variability. Surveys followed pre-determined transect patterns incorporating all major horizontal cross-members and vertical corner pilings at two depth levels: 7 m and 18 m (Love et al. 2003). The resulting species composition data were used to estimate ecological parameters typically of interest to managers, including fish density (number of fish 100 m^{-2}), biomass (kg 100 m^{-2}, calculated with established species-specific length-weight equations; Martin & Lowe 2010), and species richness.

Statistical analyses

Analyses to investigate the effects of hydrocleaning on platform-associated mid-water fish communities were based on a Before-After-Control-Impact (BACI) sampling design modified after Underwood (1993; 1994). Hypotheses about differences in fish assemblages were tested with asymmetrical distance-based permutational multivariate analysis of variance (PERMANOVA; PRIMER-E, Ltd., Plymouth, UK), a routine for testing the simultaneous response of multiple variables to one or more factors (Anderson 2001a; McArdle and Anderson 2001). This analysis tests for overall multivariate changes in community structure, which may include differences in composition, richness and/or abundances of individual species. A non-parametric procedure was used because, as with most studies of community structure, the multivariate data are not expected to meet the more stringent assumptions of traditional analyses (e.g., MANOVA). Furthermore, the power of MANOVA decreases rapidly as the number of variables (species) increases and there is no transformation available that will normalize a multivariate distribution with many zero counts (Scheiner 1993). The test statistic of PERMANOVA (*pseudo-F*) is a multivariate analogue of Fisher's *F* ratio and is calculated from a symmetric dissimilarity matrix; *P*-values are then obtained by permutation tests (Anderson 2001a, b). The primary advantage of PERMANOVA over standard rank-based non-parametric multivariate approaches (e.g., analysis of similarities, ANOSIM) is that the variation in response data can be explicitly partitioned according to complex experimental or sampling designs, including interactions among factors (Anderson et al. 2008). Asymmetrical permutational multivariate analyses of community responses to environmental impacts have already been successfully applied in other marine systems (e.g., Terlizzi et al. 2005). The assumption of homogeneity of dispersions was tested with the PERMDISP routine on data from the before period (Anderson et al. 2008).

Non-metric multidimensional scaling (nMDS; Field et al. 1982) was used to produce two-dimensional ordination plots displaying spatial and temporal variation in platform-

associated fish assemblages. All multivariate analyses were done on square root-transformed data using the Bray-Curtis similarity coefficient (Bray and Curtis 1957). This approach generally results in the more numerically dominant taxa having the largest contributions to similarity measures (Clarke 1993). The relative contribution of different fish species to observed variation in community structure was assessed with a "similarity percentages" routine (SIMPER; PRIMER-E, Ltd., Plymouth, UK) that calculates the percentage contribution of each species to the average Bray-Curtis dissimilarities between groups (Clarke 1993).

Hypotheses about overall fish density, biomass, species richness, and the densities of species with the highest relative contributions to community dissimilarity (as identified through SIMPER) were tested with univariate asymmetrical analyses of variance (Underwood 1993; 1994). Assumptions of additivity, homogeneity of variances, and normality were evaluated with interaction plots (before period) and residuals plots (Smith et al. 1993); where variances showed significant heterogeneity, the data were transformed using a $\ln(x + 1)$ function (Sokal and Rohlf 2011). Univariate analyses were done with SAS software, Version 9.3 (SAS Institute, Inc., Cary, NC).

Results

With respect to fish community structure, there was no evidence of differences in multivariate dispersions among platforms in the before period (PERMDISP, $F_{3, 24} = 2.16$, $P = 0.278$), suggesting that the samples are exchangeable under a true null hypothesis (Anderson et al. 2008). A significant interaction was not detected among control platforms on the San Pedro Shelf before the November 2007 hydrocleaning event and the period after the event (test of B × C; Table 1A), but a significant interaction was detected between platform Elly and the other platforms between periods (test of B × I; Table 1A).

These results show that the community structure did not vary significantly among the control platforms before and after the November 2007 hydrocleaning even; however, there was a significant interaction in the difference between Elly and the other platforms before hydrocleaning compared to after. Therefore, removing the invertebrate layer from an offshore petroleum platform with high pressure water had a statistically significant impact on the associated mid-water fish assemblage. This is also shown in the nMDS results where overlapping fish assemblages are present among all platforms prior to hydrocleaning (Fig. 2A), but clear differences among communities at platform Elly, compared to the others, are present after the event (Fig. 2B). While there was no evidence of a statistical interaction among the control and impact platforms before the hydrocleaning event, there was a significant interaction among locations after the disturbance. These results are consistent with the idea that the hydrocleaning event was a significant source of disturbance to the local fish assemblages at platform Elly. Total fish density (Fig. 3) and species composition (Fig. 2B) at platform Elly were back within the range of variability of the control platforms within ten months following the hydrocleaning event (September 2008).

As with fish community structure, there were consistent differences among platforms in overall fish densities after hydrocleaning. Although no significant interaction was detected among control platforms between periods (test of B × C; Table 1B), one was detected between platform Elly and the other platforms (test of B × I; Table 1B; Fig. 3). Even so, we found no evidence that overall fish biomass or species richness were significantly affected by hydrocleaning (tests of both B × C and B × I; Table 1C, D, respectively).

Table 1. Asymmetrical multivariate PERMANOVA (entire assemblage) (A) and univariate ANOVAs (species densities, biomass, and richness) (B–F) of mid-water fish associated with petroleum platforms on the San Pedro Shelf before and after a hydrocleaning event at platform Elly. Bolded *P* values are significant at the 0.05 level.

		(A) Entire assemblage			(B) Overall density		
	df	MS	*pseudo-F*	*P*	MS	*F*	*P*
Before vs After = B	1	1972.4	–	–	0.2	–	–
Times (B) = T(B)	12	2717.9	–	–	4.1	–	–
Locations = L	3	4680.7	–	–	4.7	–	–
Impact vs Controls = I	1	7436.0	–	–	14.1	–	–
Among Controls = C	2	3303.0	–	–	0.0	–	–
B × L	3	1367.9	–	–	3.3	–	–
B × I	1	2628.1	5.54	**0.024**	7.5	11.60	**0.002**
B × C	2	737.8	1.56	0.225	1.2	1.84	0.173
Residual	36	474.3	–	–	0.6	–	–

		(C) Overall biomass			(D) Species richness		
	df	MS	*F*	*P*	MS	*F*	*P*
Before vs After = B	1	618.6	–	–	3.0	–	–
Times (B) = T(B)	12	642.2	–	–	6.3	–	–
Locations = L	3	3736.9	–	–	13.8	–	–
Impact vs Controls = I	1	2727.4	–	–	37.1	–	–
Among Controls = C	2	4241.7	–	–	2.2	–	–
B × L	3	200.9	–	–	2.0	–	–
B × I	1	56.0	0.17	0.683	3.1	1.60	0.214
B × C	2	273.4	0.83	0.444	1.5	0.74	0.485
Residual	36	329.1	–	–	2.0	–	–

		(E) Blacksmith density			(F) Cabezon density		
	df	MS	*F*	*P*	MS	*F*	*P*
Before vs After = B	1	0.05	–	–	0.08	–	–
Times (B) = T(B)	12	4.69	–	–	0.02	–	–
Locations = L	3	8.63	–	–	0.04	–	–
Impact vs Controls = I	1	24.99	–	–	0.11	–	–
Among Controls = C	2	0.45	–	–	0.00	–	–
B × L	3	4.80	–	–	0.03	–	–
B × I	1	10.49	12.98	**0.001**	0.09	8.23	**0.007**
B × C	2	1.96	2.42	0.103	0.00	0.27	0.768
Residual	36	0.81	–	–	0.01	–	–

Notes: df = degrees of freedom, MS = mean square, *pseudo-F* = multivariate analogue of Fisher's *F* ratio calculated from a symmetric dissimilarity matrix (Anderson 2001a, b), *F* = *F* ratio, *P* = *P* value.

A SIMPER analysis revealed that the six species contributing the highest percentages to the overall dissimilarity between periods at platform Elly were blacksmith (*Chromis punctipinnis*; 43%), painted greenling (*Oxylebius pictus*; 5%), cabezon (*Scorpaenichthys marmoratus*; 4%), kelp rockfish (*Sebastes atrovirens*; 4%), garibaldi (*Hypsypops rubicundus*; 7%), and California sheephead (*Semicossyphus pulcher*; 3%). With the

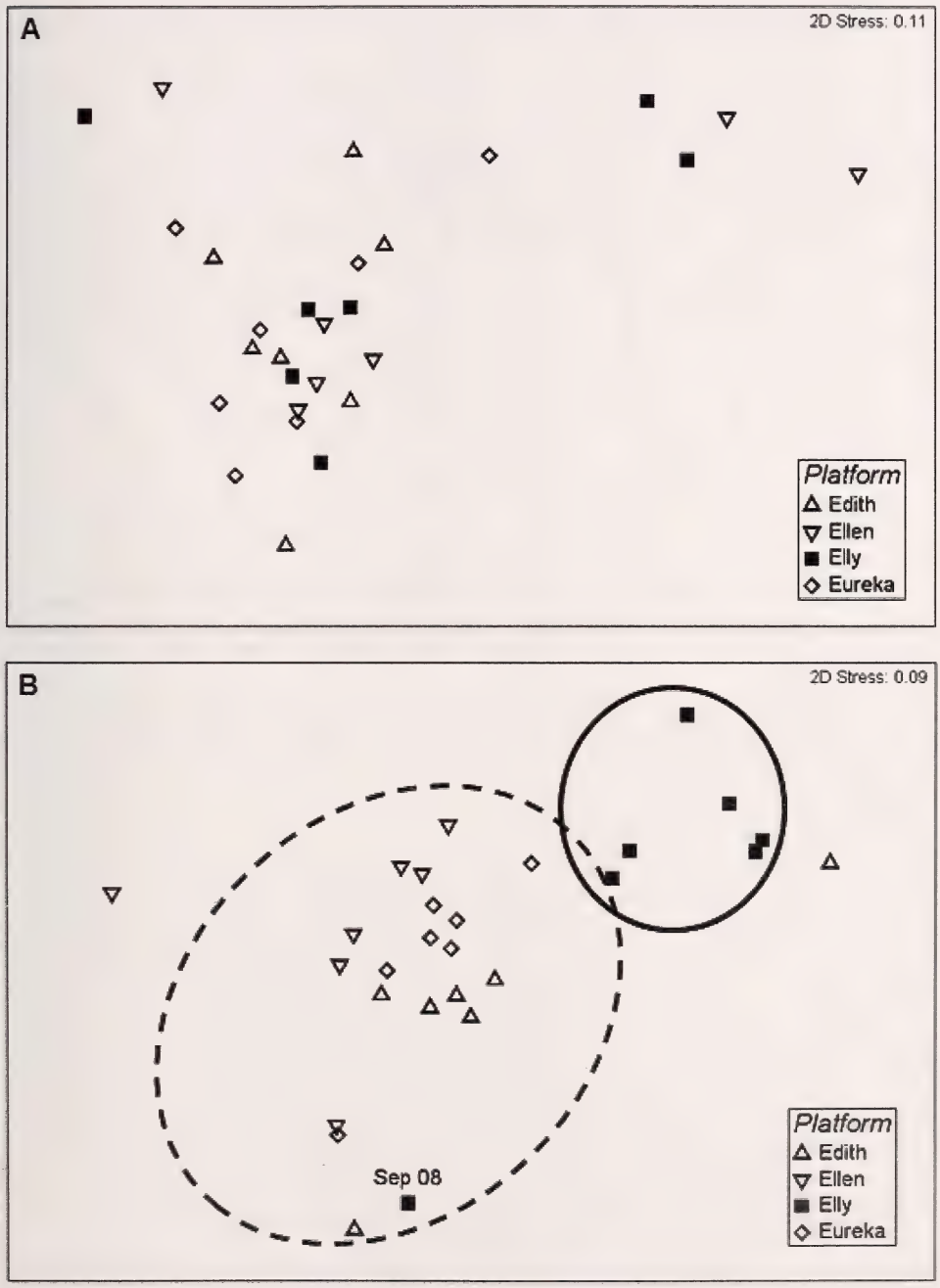

Fig. 2. Two-dimensional nMDS ordination plots comparing mid-water fish assemblages among offshore petroleum platforms on the San Pedro Shelf before (A) and after (B) a November 2007 hydrocleaning event at platform Elly. Circles drawn on graphs illustrate groups that are significantly different based on PERMANOVA results.

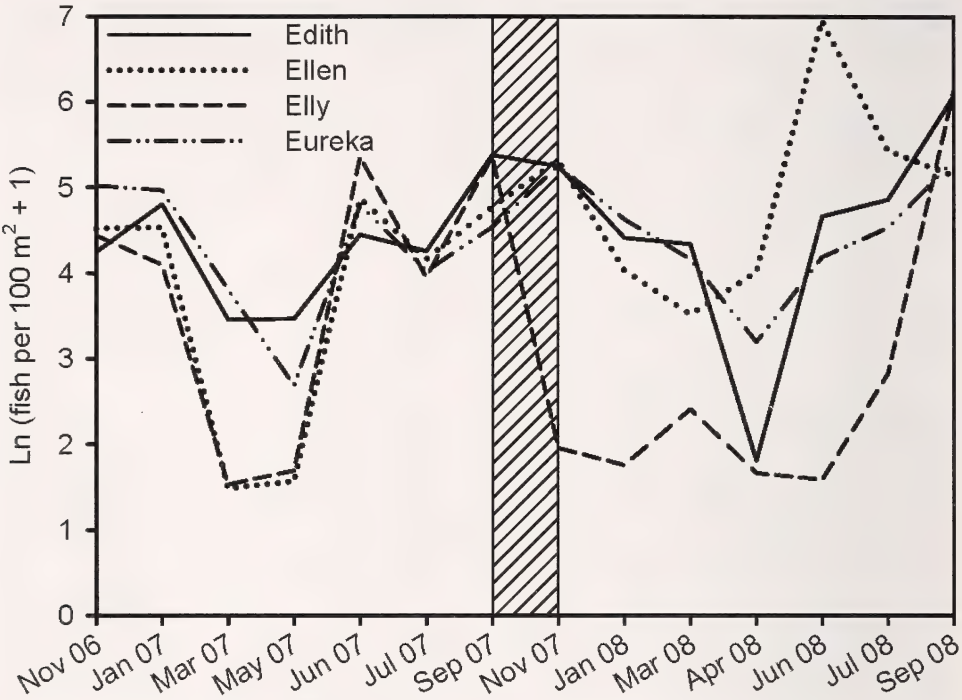

Fig. 3. A time series plot of total fish densities ($\ln(x + 1)$) at offshore petroleum platforms on the San Pedro Shelf. The hatched bar represents the timing of the hydrocleaning event at platform Elly in November 2007. The observed decrease in fish density at that platform following the disturbance was statistically significant at the 0.05 level.

exception of cabezon whose density increased four-fold, all of the species listed above decreased in abundance after hydrocleaning. Nevertheless, the observed changes in density at platform Elly were only statistically significant for blacksmith (mean ± SE Before = 58.6 ± 26.28 vs. After = 13.9 ± 10.41, $P < 0.001$, Table 1E; Fig. 4) and cabezon (Before = 0.07 ± 0.023 vs. After = 0.36 ± 0.125, $P = 0.007$, Table 1F; Fig. 4). No significant changes were in detected in these species at the control platforms (Table 1E and 1F). There was some evidence of different temporal trends in cabezon density among platforms in the before period, suggesting that the results for that species should be interpreted with some caution (Smith et al. 1993). Several other species (e.g., anchovies (*Engraulis mordax*) and Pacific sardines (*Sardinops sagax*)) also contributed to observed dissimilarities, but were only seasonally abundant.

Discussion

The rapid and intense removal of encrusting sessile invertebrates dramatically altered the community structure and total density of fish associated with the support structure of platform Elly. Blacksmith in particular exhibited a significant decrease in density following the hydrocleaning operation, separate from observed seasonal variation due to recruitment and subsequent population decline (Fig. 4). Accounting for 92% of the total fish density (although only 19% of the total fish biomass; Martin and Lowe 2010), this temperate pomecentrid was one of the main drivers of the observed post-disturbance changes in fish community structure. Blacksmith typically seek small crevices in rocky

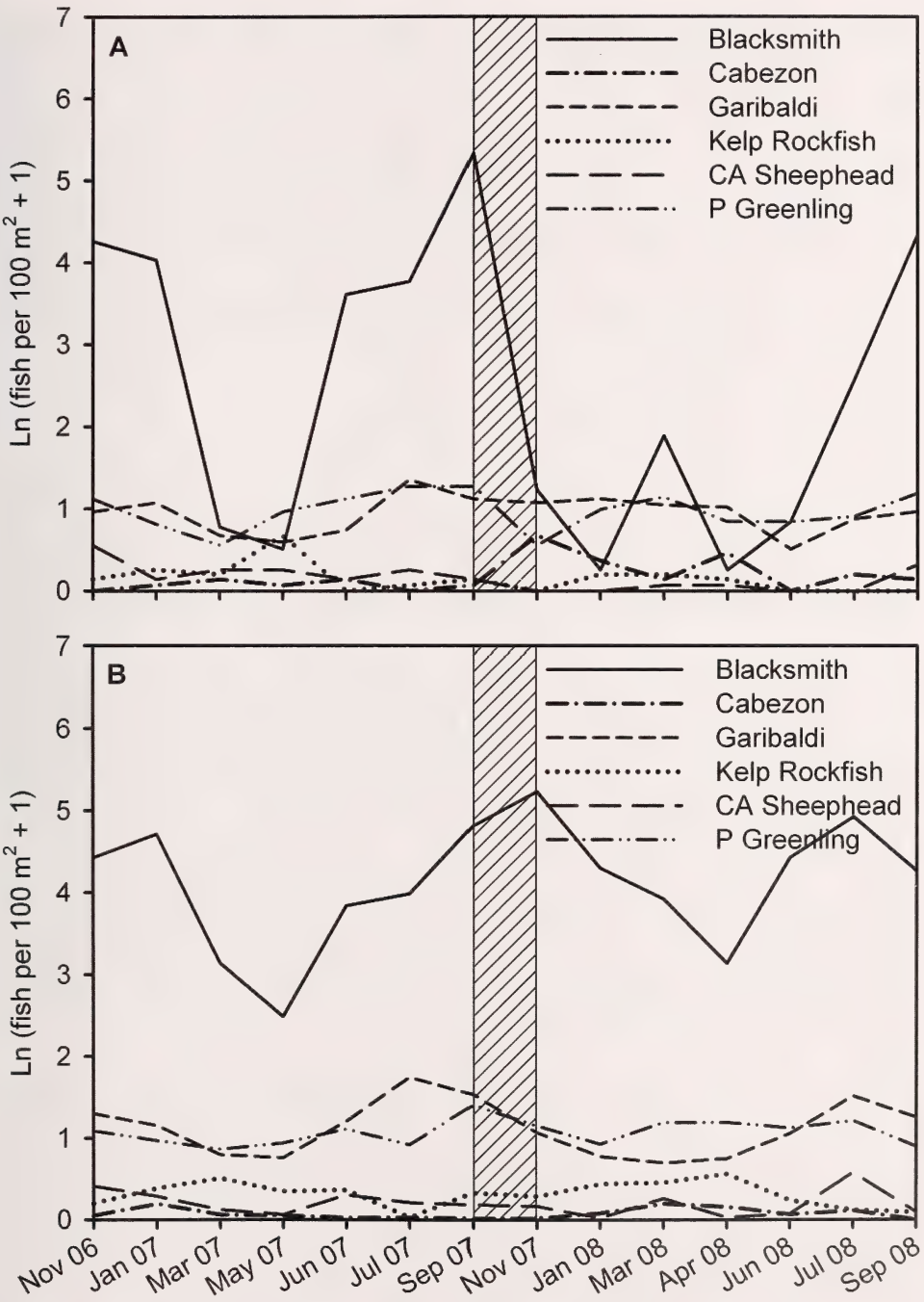

Fig. 4. Time series plot of the densities ($\ln(x + 1)$) of the fish species consistently contributing the most to dissimilarity of samples collected before versus after the hydrocleaning event at platform Elly (timing represented by the hatched bar) (A) and mean densities at the three control platforms (B).

reefs for nocturnal shelter (Ebeling and Bray 1976) and the complex invertebrate layer on the platform would have provided similar microhabitat on an otherwise smooth steel surface. The near-total removal of this biogenic habitat presumably left a large proportion of the blacksmith population vulnerable to predation and high water flow speeds. Blacksmith are a rapidly colonizing planktivorous species, providing a consistent source of food for many piscivorous fishes, including rockfishes (*Sebastes* spp.) and kelp bass (*Paralabrax clathratus*) (Limbaugh 1964). Given their numerical dominance in the mid-water fish community, any significant decrease in blacksmith densities has the potential to negatively impact the entire fish assemblage via a reduction in prey resources. Similarly, by virtue of their high abundances, blacksmith may also contribute significant amounts of inorganic nitrogen to local primary producers via ammonium excretion (Bray et al. 1986).

The lack of an observed impact of hydrocleaning on the densities of larger fish species may have been due to their utilization of habitat below 20 m depth (Martin and Lowe 2010). Acoustic telemetry data on four species (California sheephead, cabezon, grass rockfish (*S. rastrelliger*), and kelp rockfish) at these same SPS platforms have revealed that they are capable of large vertical movements at both daily and seasonal scales (Mireles 2010). Species that feed on invertebrates (e.g., California sheephead; Cowen 1986) may have been foraging in the intact invertebrate layer deeper in the water column periodically while still utilizing the shallower disturbed region for other activities. Blacksmith, in contrast, are uncommon below 20 m (Limbaugh 1964; Martin and Lowe 2010), possibly due to a thermal preference for warmer waters, increased availability of their planktonic prey near the surface, and decreased predation risk from deeper-water predatory species such as rockfish. Only one fish species, cabezon, was observed to increase in density following the hydrocleaning event. However, this result was likely due to increased visibility due to the loss of its cryptic surroundings, rather than an actual increase in local abundances (Willis 2001).

The observed recovery of blacksmith densities (and as a consequence, overall fish community structure) within ten months of the hydrocleaning operation coincided with the rapid re-establishment of mussel beds on the disturbed structure (pers. obs.), suggesting that the shallow-water invertebrate layer associated with the SPS petroleum platforms is particularly important habitat for this species. The invertebrate assemblages on both offshore oil platforms and natural rocky reefs are an important source of prey to microcarnivorous fish like blacksmith (Page et al. 2007) and increases in substratum rugosity and provision of shelter have been shown to be positively related to the density and biomass of many other fish species (e.g., Friedlander and Parrish 1998). In addition to supplying food and shelter, the platform invertebrate layer may also contribute directly to increased reproductive success of local fish populations. Spawning aggregation sites of at least one temperate pomacentrid are characterized by higher substratum rugosity than non-spawning sites (Gladstone 2007) and two fish species, including the pomacentrid garibaldi, were observed protecting egg masses embedded in the invertebrate layer at the SPS platforms (Martin and Lowe 2010).

Hydrocleaning, a high-intensity but temporally discrete event, drastically altered the shallow subtidal invertebrate assemblage at platform Elly, and in turn, the structure of the associated fish community. Even so, the system appears to be resilient, recovering to pre-disturbance conditions within ten months. Presumably this is due in part to the rapid recruitment and growth of both sessile invertebrates and the numerically dominant blackfish on the platform. Our results provide some insight into the potential limitations

to resilience if disturbance events were to increase in frequency through time. Clearly, if disturbances such as the one produced by hydrocleaning were to happen more frequently than once per year, it is unlikely that the associated biological community would fully recover before the next event, presumably leading to a decrease in overall biodiversity (Connell 1978). It would also be interesting to know how the recovery trajectory of the local community might be altered if fish with life-histories markedly different from blacksmith were affected by a given disturbance (e.g., longer-lived or low-recruiting species), or how disturbance might alter other aspects of fish ecology such as diet or habitat utilization.

Although the desirability of temporally and spatially well-replicated sampling both before and after a disturbance event is widely accepted given the high degree of spatial and temporal variability inherent in natural systems (Underwood 1993; 1994), there are significant practical constraints to accomplishing this goal. In general, it is difficult (if not impossible) to know where or when a disturbance might take place or their potential magnitude and spatial extent, so the degree of pre-disturbance sampling tends to be quite limited. Hydrocleaning and other planned or routine disturbance events provide an important opportunity to investigate the effects of disturbance on natural populations and communities. Our results show that a well-replicated BACI sampling design can detect even subtle biological changes in response to disturbance. We also found that taking a multivariate approach to data analyses provided insights that would have been lost had we used only more traditional univariate statistics. For example, there was no evidence of an effect of hydrocleaning on species richness, although community composition overall was actually quite different for some time afterwards. While not explicitly addressed in our study, it is likely that functional diversity and associated ecosystem processes were also changed in response to the disturbance, given the observed changes in community composition (Micheli and Halpern 2005; Suding et al. 2008).

Widespread human impacts on the marine environment are significantly altering biodiversity from local to global scales (Jackson et al. 2001; Myers and Worm 2003; Pandolfi et al. 2003). Documenting such impacts is a key first step towards developing a mechanistic understanding of community disassembly in the face of increasingly frequent and intense perturbations (e.g., Easterling et al. 2000). Such knowledge will be critical to our ability to successfully protect and restore biological communities in the future.

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Factors Affecting Courtship Success and Behavior of a Temperate Reef Fish, *Brachyistius frenatus*

Jesse S. Tootell and Mark A. Steele

Department of Biology, California State University, Northridge, CA 91330-8303, mark.steele@csun.edu

Abstract.—Size can play an important role in determining reproductive success through the establishment of dominance hierarchies and mate selection. We explored the relationship between size of individuals and courtship success in the kelp perch, *Brachyistius frenatus*, off the coast of southern California at Santa Catalina Island. Courtship displays were timed and the length of the interaction was used as a proxy for courtship success. In addition, we observed how much of their time individuals spent performing different activities throughout the day in two adjacent habitats dominated by different macroalgae. We found that body size played a significant role in determining the success of courtship. Large males were slightly more successful than small males, but the male: female size ratio was the best predictor of mating success of male *B. frenatus*, with males that were large relative to the female they were courting being most successful. Time allocated to different activities varied significantly with time of day and habitat. A greater proportion of time was spent on foraging in the morning than in the afternoon, and females spent more of their time foraging than did males. Behaviors other than foraging were only observed in one habitat type (understory algae) and courtship behavior was only observed during the afternoon. Smaller males tended to spend more time searching for receptive females than did larger males.

Introduction

Reproductive success of fish is often a function of size, which can play an important role in determining males' access to females through the mechanisms of mate selection or territoriality (Warner, 1982; Hoffman, 1985). The significance of size also varies depending on the reproductive strategies and morphologies of different fish groups. With only a few unique exceptions in fishes (Bisazza & Pilastro, 1997), larger individuals are generally favored in mate selection for various reasons, but most often because larger females are more fecund and larger males are better able to defend limited resources such as nesting sites or food (Schmale, 1981; Donhower & Brown, 1983; Hughes, 1985; DeMartini, 1988). Body size often has a heritable component and so selection of large mates may produce more fit offspring (Hanson & Smith, 1967).

The family Embiotocidae contains species that are viviparous gonochores and several studies have examined reproductive behavior of members of this family (e.g., Hubbs, 1917; Hubbs, 1921; Shaw & Allen, 1977; Darling, 1980; Hixon, 1981; Baltz, 1984). Only one study (DeMartini, 1988), however, has examined the reproductive behavior of *Brachyistius frenatus*, the subject of this study, in any detail. *Brachyistius frenatus* (kelp perch) is a temperate reef fish that is part of the assemblage of temperate rocky reef fishes

* corresponding author: *mark.steele@csun.edu*

in southern California (Stephens et al., 2006). As a viviparous species, it has different mating and dispersal patterns than egg-spawning fishes (Hubbs & Hubbs, 1954). Relatively little is known about the courtship behavior of *B. frenatus*. Males can reach sizes equal to those of females, and males are thought to be territorial (Hubbs & Hubbs, 1954; DeMartini, 1988). Females are polyandrous, and agonistic male-male interactions are common, suggesting direct competition for mates or mating territories (DeMartini, 1988). Although it is not clear which resources may be valued, other embiotocids have been shown to establish territories for food and mating sites (Hixon 1981).

The general goals of this study were to explore the courtship behavior of *B. frenatus*, how it is influenced by size, and how allocation of time to courtship influences foraging behavior. Specifically, we (1) evaluated whether body size of males and females influenced courtship success of males; (2) tested how male body size influenced time spent on courtship and time spent searching for mates; (3) tested whether time spent foraging differed between males and females as a consequence of different allocation of time to mating activities by the two sexes; and (4) evaluated whether mating and foraging activities were restricted to particular habitats or times of day.

Methods

Observations of *B. frenatus* were conducted over two weeks in mid November 2010 in Big Fisherman Cove (BFC) on Santa Catalina Island, California. BFC is inside a state marine reserve. Our study was restricted to this single site and time period due to logistical constraints. All evaluations of kelp perch behavior were done on snorkel in water 1.5–5 m deep. The habitat at this site abruptly shifts from *Macrocystis pyrifera* (giant kelp) dominated (deeper) to understory algae dominated rocky reef (shallow) within this depth range. The understory algae include the algae *Eisenia arborea, Asparagopsis taxiformis, Plocamium cartilagineum, Sargassum* spp., and other non-canopy forming species. The observations were divided into two main types: courtship interactions and time budgets.

Courtship Observations

Courtship in *B. frenatus* consists of the male moving into position above the female and performing a display in which his whole body quivers vigorously. The female often stays in motion during his display and the male must then maintain position while continuing to twitch its body. In the most successful courtship interactions, the male will move the ventral side of his body towards that of the female to bring the sexual organs into contact.

During courtship observations (n=53), the size of both the male and female participants was estimated visually to the nearest cm, and the interaction was given a numerical score representing the relative success of the mating attempt. The following criteria were used: if the male was rejected by the female immediately upon his display (i.e., she quickly swam away and did not allow the male to move into position above her), then the interaction received a 1. If the interaction lasted for between 2–15 seconds, then it received a 2. If it lasted 15–30 seconds it received a 3, and if it lasted for 30–45 seconds it received a 4. If there was an apparent copulation (regardless of duration), or if the mating display lasted for more than 45 seconds, then it received a 5.

Time Budgets

Time budgets were constructed for 63 fish to establish a basic understanding of how kelp perch allocate time amongst different activities. The observations were done in both

habitat types (*Macrocystis* and understory algae) during two time periods: morning (07:00–11:30) or afternoon (13:00–16:00). Individuals were observed for between 5 and 10 minutes. The activities recorded were courtship, foraging, roaming, agonistic display/chase, and the number of mating attempts. Agonistic displays consisted of two males aligning themselves head to tail with their mouths open, fins erect and the body slightly flexed toward the opponent. Courtship was defined as the act of performing courtship displays, foraging as slow movement with active feeding as evidenced by protrusion of the jaws, and roaming as fast movement with no feeding. Roaming appeared to be done only by males searching for mates and it was often followed by a courtship attempt. Therefore, courtship and roaming were combined into a single response variable for some analyses. All activities were analyzed as percent of the total time observed.

Because of the morphological similarities between male and female *B. frenatus*, the only ways to determine the sex of an individual were to observe the gonopodium on the anterior portion of the anal fin, which was often difficult to see due to light conditions or viewing angle, or to observe the fish in a mating or agonistic interaction. In the closely related shiner perch (*Cymatogaster aggregata*) and other embiotocids (Hubbs, 1917; Shaw & Allen, 1977; Hixon, 1981), only males are involved in agonistic chasing and displays and only males engage in the aforementioned quivering during courtship, so these behaviors were used to identify males when the gonopodium could not be seen. Data from those individuals that were observed but that could not be sexed were excluded from analyses of behavior related to courtship or agonism.

Statistical Analysis

To evaluate the relationship between body size and courtship success, three separate logistic regressions were used. These regressions tested whether courtship success (categorical courtship score) was a function of either male size, female size, or the male: female size ratio.

To explore how behavior patterns were related to size, sex, habitat, and time of day, time budget data were analyzed in different ways to address different questions. Response variables included % time foraging (both sexes), % time engaged in roaming + courtship (males only), and % time roaming (males only). The percent of time spent on courtship and agonism was so low that these behaviors were not statistically analyzed. To test whether time spent searching for mates was related to male body size, we used linear regression to test the relationship between percent of time spent roaming and male body size. To test whether the % of time males spent on mating activities (roaming + courtship) was influenced by time of day, we used a two-sample *t*-test to compare data from males in the morning versus afternoon in the understory habitat (the only habitat in which mating activities occurred). A two-way analysis of variance (ANOVA) with Time and Habitat as fixed factors was used to test whether the % of time spent foraging differed between time periods or habitats. This analysis included the entire time budget observations, including those in which sex of the individual could not be ascertained. A subset of the time budget data set, those observations in which gender had been determined, were evaluated with analysis of covariance (ANCOVA) to test whether % time spent foraging differed between sexes (a fixed, categorical factor) or varied with body size (a covariate). Analyses involving gender as a factor, and those restricted to a single gender, used only data collected in the understory habitat, because this habitat was the only one in which fish could be reliably sexed. Time budget data did not meet the assumption of normality, and transformation did not improve their distribution. We proceeded with parametric

analyses on untransformed data, nevertheless, because ANCOVA and ANOVA are generally robust to violations of normality (Gotelli and Ellison 2004).

Results

Mating Interactions

Males were more successful at courtship when females were small relative to them, as indicated by a significant positive relationship between courtship success score and the male: female size ratio (Fig. 1A; $df=4$, $\chi^2=40.29$, $p<0.001$). Although courtship score tended to increase with male size and decrease with female size (Figs. 1B and 1C), neither relationship was statistically significant ($df=4$; $\chi^2=7.48$, $p=0.112$; $\chi^2=7.67$, $p=0.105$, respectively), emphasizing the importance of the ratio of male to female size. Only two copulations were observed, and these occurred between pairs with male: female ratios of 12:10 cm and 14:14 cm.

Time Budgets

Courtship, agonistic interactions, and roaming were only observed in the understory algae habitat (Fig. 2). Here, courtship + roaming accounted for a higher proportion of total activity in the afternoon than in the morning ($t=3.6$, $df=18$, $p=0.002$). The % time spent foraging also differed significantly between times of day, as well as between habitats (Table 1, $p<0.05$). The increased time spent on mating activities in the afternoon resulted in a lower % of time spent foraging in the afternoon than in the morning. A greater % of time was spent foraging in the *Macrocystis* habitat than in the understory algae habitat where mating behavior occurred. For % time foraging, there was a significant interaction between habitat and time of day because foraging was the only behavior that occurred in the *Macrocystis* habitat, whereas changes between time periods in the percent time spent on various behaviors did occur in the understory habitat. Foraging accounted for 100% of activity of *B. frenatus* when observed in the *Macrocystis* habitat, but in the understory algae habitat it accounted for only 68% of time in the afternoon and 90% in the morning.

Agonistic interactions occurred even in the absence of courtship during the morning, but accounted for about half as much of the time budget during this time as they did in the afternoon (~4.2% and 8.5% respectively). Several times during courtship, males were interrupted by agonistic males. The interruption was always performed by a male of equal or larger size and the interrupting male sometimes courted the female in the broken pairing. Agonistic displays were also never performed by two disproportionately sized males. When chasing occurred, larger males always chased smaller males.

Foraging behavior differed between the genders. Females spent more of their time foraging than males (means ± SEM of 93% ± 5.9 vs. 73% ± 4.8 for females and males, respectively; $F_{1,30}=6.8$, $p=0.01$). Females did not engage in agonistic displays or roam, and thus spent all of their time foraging when not being courted. There was no detectable relationship between size and time spent foraging ($F_{1,30}=0.0$, $p=0.86$).

There was some evidence that male size affected roaming behavior. Small males tended to spend more time roaming than larger males (Fig. 3)($r^2=0.15$, $F_{1,18}=3.2$, $p=0.08$).

Discussion

This study reveals a clear relationship between courtship success and the size of males relative to females in *Brachyistius frenatus*. Females spent significantly more time being courted by males of equal or larger size than themselves than by smaller males, indicating that the relative size of male and female partners was likely a good predictor of

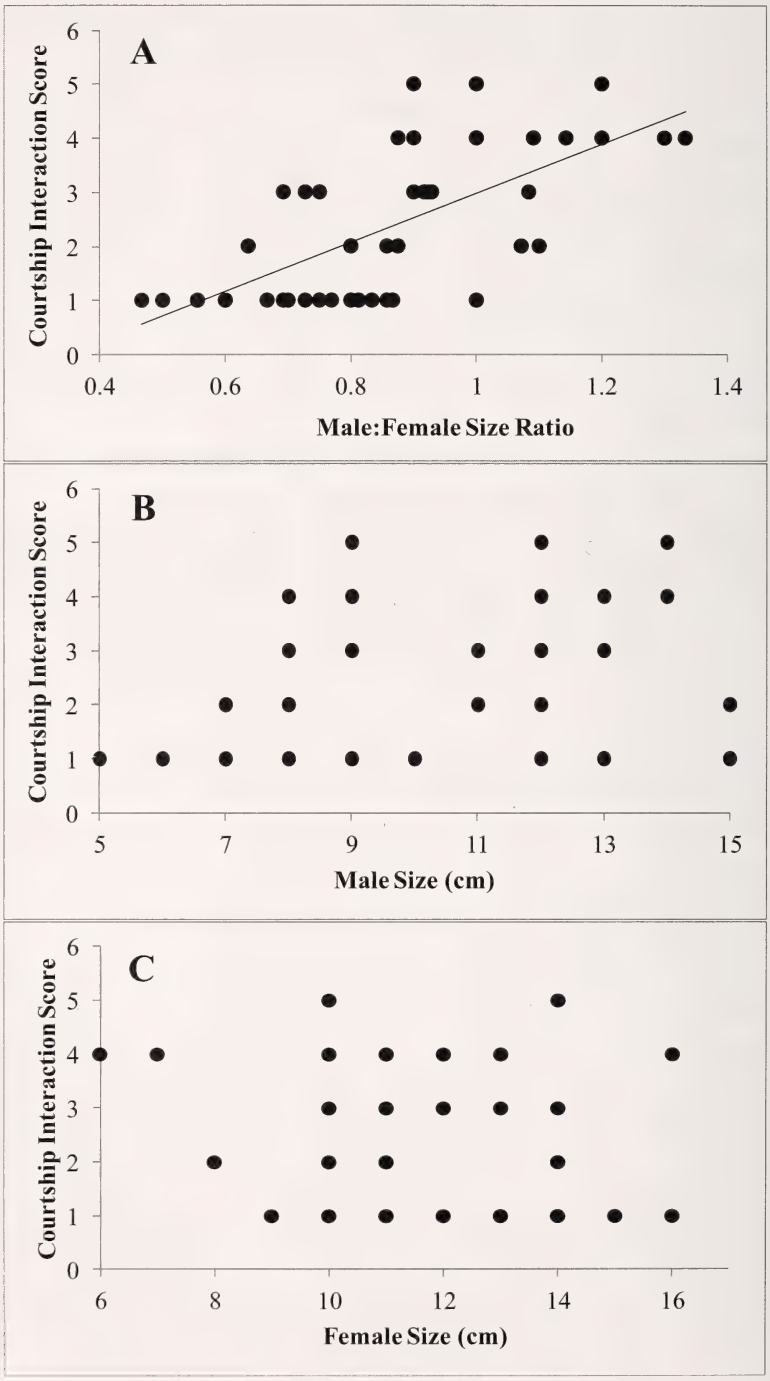

Fig. 1. Relationships between courtship score and A) male:female size ratio, B) male size, and C) female size and for $n=53$ total interactions.

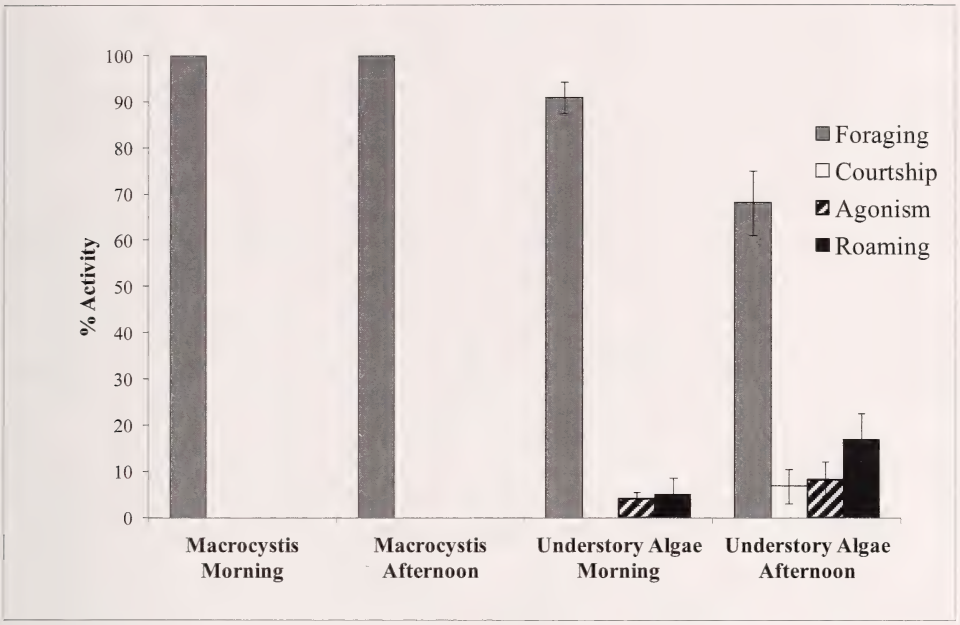

Fig. 2. Percent of time allotted to each activity by *Brachyistius frenatus* in two habitats at two times of day. Bars represent ± 1 SEM. For *Macrocystis* during afternoon $n=15$, *Macrocystis* during morning $n=15$, understory algae during afternoon $n=17$, and for understory during morning $n=16$.

probability of mating. Somewhat unexpectedly, absolute size of males was not a particularly good predictor of courtship success, with larger males being only slightly more successful than smaller males. However, it should be noted that some of the large males that had poor courtship success were also courting very large females. DeMartini (1988) found that all males preferentially courted large females, but the present study reveals that an apparent preference by females for males larger than themselves renders courting efforts of relatively smaller males ineffective. Those smaller males, however, successfully courted females that were smaller than them. It appeared that all mature males were capable of mating, but high courtship success was only attained with a female of equal or lesser size. Therefore, the success of any given male is less a function of its absolute size and more related to its size relative to accessible females. Consequently, male reproductive success appears to be limited by the number of females in the population that are of equal or smaller size. This finding differs somewhat from the size-assortative mating documented in the closely related species *Micrometrus minimus* (Warner & Harlan, 1982) and *Cymatogaster aggregata* (DeMartini 1988), in that *B.*

Table 1. Results of factorial ANOVA testing for differences in the % time spent foraging by *B. frenatus* (males and females combined) during two time periods (morning and afternoon) and in two habitats (*Macrocystis*) and understory algae).

Source	df	*F*	*P*
Time	1, 59	7.5	0.008
Habitat	1, 59	24.7	<0.001
Habitat*Time	1, 59	6.6	0.008

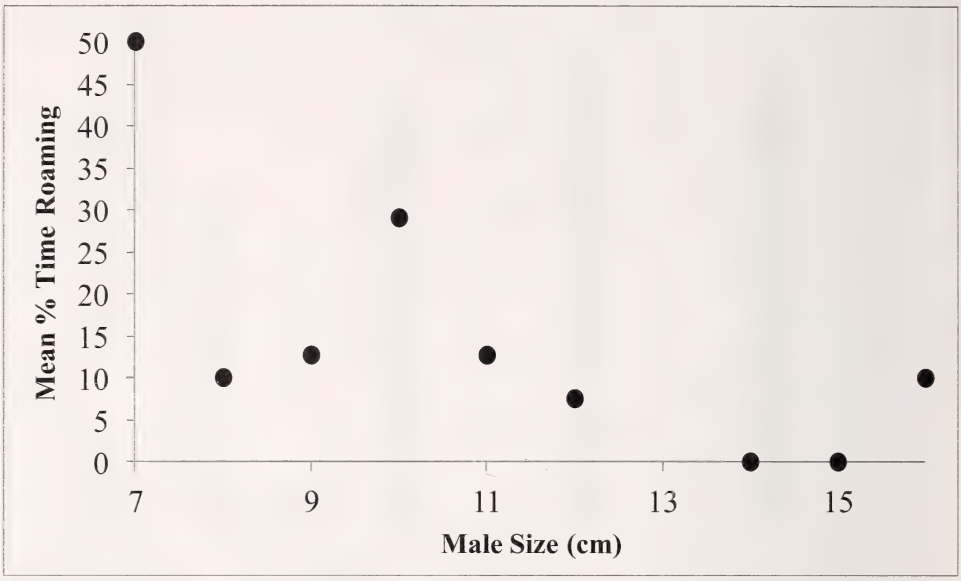

Fig. 3. Relationship between size and % of time spent roaming by male *Brachyistius frenatus*; $n=20$.

frenatus males will successfully court females similar in size and ones smaller than themselves.

Time budget observations revealed some evidence of a relationship between male size and time spent roaming, where smaller males roamed more often. This increased roaming may be a result of agonistic male-male interactions which forces small males to spend more time moving to avoid conflict with larger males, or smaller males may have to travel farther or more often than larger males in order to find receptive females. Regardless of the cause, since smaller males appear to roam more frequently, be slightly less successful during courtship than larger males, and perhaps mate with smaller females that will produce fewer offspring than large females, small male *Brachyistius frenatus* must have lower reproductive success than larger males.

The fact that aggressive interactions between males continued in the absence of courtship activity and only in the habitat where courtship occurred (understory algae) and not in the habitat used solely for feeding (giant kelp) indicates that agonism in kelp perch is primarily used as a mechanism to defend mating sites and access to females. DeMartini's (1988) study of kelp perch supports this conclusion, as do several other studies of embiotocid species, which have revealed similar aggressive behavior in males (Hubbs, 1921; Shaw & Allen, 1977; Hixon, 1981). The observations of male interruptions and agonism suggest that male-male interactions are governed by a size-based dominance hierarchy predicated on access to females, as has been widely noted in other fishes (e.g., Robertson & Choat, 1974; Downhower et al., 1983; Warner & Schultz, 1992). Because females did not search for mates (roam) or engage in agonistic interactions, they were able to spend more of their time foraging than were males.

It appeared that male size affected roaming behavior, though this pattern was marginally non-significant. Further study with higher replication may elucidate the actual associations between these factors in *B. frenatus*. Furthermore, previous work on marine fishes has shown that different size classes within a species may mate at different times of

the year (Hubbs, 1921; Baltz, 1984; Shultz, 1991), so repeated observations over a longer time period would be valuable in addressing this possibility in kelp perch.

It is noteworthy that courtship was only observed in the understory algae habitat and not in the *Macrocystis* bed habitat, especially given that the study species is called the *kelp* perch and DeMartini (1988) observed courtship in this species exclusively in giant kelp canopy. We suspect that this finding reflects mating habitat preferences that will only be expressed when *Macrocystis* and understory algae habitats are in close proximity, as was the case at our study site. At reefs surrounding Catalina Island, Anderson (1994) noted that adult *B. frenatus* were proportionally more abundant in understory algal habitats than were newly born offspring, which were found almost exclusively in the *Macrocystis* canopy habitat. One might therefore suspect that our finding of courtship occurring only in the understory algae habitat was the result of adults only occurring in this habitat and juveniles only in the *Macrocystis* habitat. This explanation, however, is incorrect. Adults were present in both habitats and there was no significant difference between the sizes of *B. frenatus* seen in the two habitats. The study sites at which DeMartini (1988) noted courtship behavior of *B. frenatus* occurring in the *Macrocystis* canopy habitat were much deeper (approximately 15 m) than our study site, and so the understory algae habitat was both more distant (vertically) from the canopy habitat and likely more sparse due to shading by giant kelp.

Results from this study conform to a common trend in marine fishes where larger mates are often preferred. Male preference for larger females is well documented and expected, as larger females are more fecund. Similarly, in species where males perform some role beyond fertilization for which large size is advantageous (e.g., defense of a nest site or offspring), larger males are expected to be preferred by females. DeMartini (1988) found that *B. frenatus* males prefer larger females and the present study indicates that large females also prefer larger males. Given that male *B. frenatus* do not defend their offspring nor provide females access to any limited resource, females may prefer larger males because their offspring are more fit, whereas males may choose larger females because they produce more offspring.

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Fishing off the Dock and Under the Radar in Los Angeles County: Demographics and Risks

Ana Pitchon[1] and Karma Norman[2]

[1]*Department of Anthropology, California State University-Dominguez Hills, 1000 East Victoria Street, Carson, CA 90747, apitchon@csudh.edu*
[2]*NOAA Fisheries, Northwest Fisheries Science Center, 2725 Montlake Blvd East, Seattle, WA 98112-2097, karma.norman@noaa.gov*

Abstract.—The research presented here represents an analysis of pier-based subsistence fishing in Los Angeles County. The researchers conducted surveys and participant observation at 4 field sites on Los Angeles piers. Subsistence fishing among populations in the mainland United States has been neglected as a significant activity of research interest. This may be in part because individuals engaged in subsistence fishing are often members of long established poor, indigenous or diasporic communities. With this project, we analyzed particular marine cultural phenomena, otherwise invisible in a highly bureaucratized system of fisheries management and risk analysis, by researching and describing some of the fishing practices and fishers of Los Angeles County's piers. Ethnographic survey research reports on the unique demographics, risk perceptions, and sociocultural aspects of distinct pier-based fishing communities in Southern California.

Introduction

The nutritional abundance found in relatively wealthy nations, and their concomitant rise in obesity rates, is often contrasted with malnutrition and even famine elsewhere. But, as officials at the World Food Program have noted, a "silent tsunami" finds food price inflation worrying almost every nation, and food insecurity is spreading unevenly into new and unanticipated geographies. Food insecurity, while not necessarily a new phenomenon in some parts of the world, has taken on more urgency as it has begun to touch traditionally wealthy nations (Clemmitt 2008). Important new stressors include climate variability and change, agricultural practices which focus on alternative fuels over food products, and the ubiquity of troubled economies.

Fisheries resources are often cited as key components in maintaining world food security (Kent 1997; Garcia and Rosenberg 2010). This notion is reinforced by the worldwide consumption of seafood, which increased from an estimated 1976 total of 27 pounds per capita to 33.5 pounds per capita in 1996 (FAO 2000). Maintaining a consistent supply of seafood, however, is achieved by intensifying exploitation through commercial fishing, increasing production of the resource through hatchery programs or even supplementing wild resources with farmed species (Bailey et al. 1996; Naylor 2006). As wild catches decrease in volume (Myers and Worm 2003), new species are suddenly considered palatable, and hatchery production increases, as it did in the 1990s and 2000s (FAO 2005). Such large-scale projects mean little at the household level, where people still have to buy these foods, and where the seafood products available are often species destined for elite markets (Pitchon 2001). Non-commercial fishing in U.S. lakes, rivers, and coastal waters is often characterized as recreational, but given rising food and energy costs, this type of fishing can represent much more than a pursuit conducted for its own sake.

Food insecurity is defined as limited or uncertain access to enough quality food for a healthy life (Harrison et al. 2007). In terms of food, definitions of security stress the "assured ability to acquire acceptable foods in socially acceptable ways (that is, without resorting to emergency food supplies, scavenging, stealing, or other coping strategies)" (USDA 2006). Fishing for consumption, while generally accepted socially as compared to other coping strategies, can nevertheless be triggered by lack of access to retail food supplies, thus suggesting that the activity may be an indicator of food insecurity.

In this project, we analyzed a particular marine cultural phenomenon, otherwise invisible in a highly bureaucratized system of fisheries management, by researching and describing some of the fishing practices and fishers of Los Angeles County's piers. Our multi-sited ethnographic survey research revealed the unique demographics, risk perceptions, and sociocultural aspects of distinct pier-based fishing communities in Southern California. The research presented here puts forward an analysis of pier-based subsistence fishing in Los Angeles County as a possible food insecurity coping strategy. Our research team conducted surveys and participant observation at 4 field sites on Los Angeles piers, where pier-based fishing and catch preparation and consumption are evident.

For this project, we further identified the extent to which "recreational" angling is being pursued as a form of "subsistence" fishing. As with the Alaska Department of Fish and Game, we take subsistence fishing to be defined as the "use of wild, aquatic resources for noncommercial, customary and traditional uses for a variety of purposes, specifically the direct personal or family consumption as food," although we recognize that others have argued for an expanded notion of subsistence fishing (Schumann and Macinko 2007). The objective was to understand the drivers behind these activities, in urban areas, from the vantage points offered by the collection of sociocultural and demographic data. Issues of ethnicity, citizenship, poverty, and food insecurity were variables of interest in our research. We were also interested in the persistence of fishing and catch consumption activities despite warnings about heavy metals and contaminants that could be consumed along with harvested aquatic species.

Applying an anthropological approach to urban subsistence fishing in California, we researched these questions through a variety of methods, pulled not only from anthropology and its relatively recent emphasis on multi-sited ethnography (Marcus 1995), but from related social science disciplines (see Table 1).

Methods

Methodological Overview

We began this research with the assertions that pier anglers in LA County 1) represent low income populations, and that, accordingly, they are 2) fishing from piers to meet subsistence and income needs. In order to examine these two suppositions concerning pier fishing, we conducted three months of field work at four pier sites in Los Angeles County.

Eighty-eight pier fishers were subjected to both unstructured interviews as well as a formal survey instrument consisting of forty-five questions. Our survey included questions covering fishing habits, demographic information and, importantly, the dietary significance of the catch. Detailed field notes included other relevant information not covered in the survey, and such information was largely collected during open and semi-structured interviews that accompanied the formal survey. Qualitative ethnographic data

Table 1. Research methodologies employed in Los Angeles County pier fishing study.

Multi-sited Ethnographic Methodologies	• Semi-structured interviews • Unstructured interviews • Participant observation • Assessments of the social characteristics of anglers in site-specific cultural contexts
Demographic Methodologies	• Collection of quantitative demographic baseline data • Identification of sub-populations consuming toxin-exposed fish and shellfish
Sociological Methodologies	• Identification of fishermen cohorts • Descriptions of social conditions and fishing practices particularly as they relate to need and food security
Risk Analysis and Perception Methodologies	• Assessments of the awareness and perception of contamination of fishing sites • Data collection on the stressors and behaviors within affected fishing groups

was considered in conjunction with the quantitative survey data we collected, in order to provide a more comprehensive and holistic analysis.

Johnson (1998) used the term '*exploratory-explanatory approach*' to describe the sequencing of open-ended and structured methods for testing hypotheses about cultural beliefs and value systems. The two phases of research inherent to Johnson's approach as well as the research presented here pursue different but complementary goals, and have different information-eliciting methods and different sampling strategies. Approaching the qualitative and quantitative segments individually during the data collection phase allowed for a more comprehensive final product. We balance the contextual detail against the predictive power and comparability of results required to examine our two distinct, yet interrelated assertions. Previously, researchers, such as Kempton, Boster and Hartley (1995) and Boster and Johnson (1989), have found success in combining open-ended ethnography and structured questionnaire research to draw on the strengths of both approaches.

Exploratory Phase

The individuals of interest in our research were the shore-based fishers in Los Angeles County, and the target population specifically included those who were engaged in fishing from piers. We began the exploratory phase by observing and establishing fieldsites, establishing key informants through purposive sampling, and conducting unstructured, in-depth interviews about their social and economic circumstances. This phase constituted the ethnographic portion of the research, providing detail on cultural variables that drive pier-based angling but cannot be ascertained through more formal, structured surveys.

Explanatory Phase

The explanatory phase began with a sampling procedure to identify and secure representative groups of individuals for study. A limited sampling frame was not feasible given the absence of a comprehensive list of anglers from either fishing licenses or other sources, and public pier fishing in California is not typically licensed. We therefore used

an intercept technique that allowed for representation of the multiple ethnic populations within the study locations, and for the best available sampling approach (Bernard 2002).

The survey questionnaire was designed to gather information needed to address the specific objectives identified within the project's inception. The questionnaire included questions on ethnicity, income, education, age, fishing frequency, amount of fish consumed, types of fish consumed, preparation and cooking methods, others in the household consuming the catch, and awareness and knowledge of the state's health advisories vis-à-vis locally caught seafood.

In addition to demographics, this research revealed socio-cultural and risk characteristics associated with fishing activities, including potential exposure to toxicity. We also examined risk perceptions associated with the consumption of local catch, qualitative data on cultural identities and expressions of cultural community, and economic incentives regarding subsistence fishing. These data may inform culturally appropriate advisories to high-risk sub-populations of fishers.

Study Sites

Los Angeles County is not known for its idyllic fishing grounds and, in a sprawling, highly urbanized context, environmental threats are often competing for public attention with a host of salient concerns. Despite its place as the second largest urban hub in the U.S., however, Los Angeles County is home to communities of people who directly depend on the region's natural resources for sustenance and otherwise.

As a region with a notably high cost of living, high rates of immigration, and, accordingly, well documented issues related to localized food insecurity, Los Angeles County represents an appropriate location to investigate the subculture of subsistence living. In order to provide a suitable view on subsistence fishing activities in Los Angeles County, we selected four field sites that served as representative illustrations within the County (Fig. 1). The study piers were and are frequented by diverse racial and ethnic groups.

Many pier fishers and study participants do not live in the city in which they fish, and so the piers themselves, as locations of the activity of interest, served as the centers for community identification and our attendant survey work. With respect to subsistence harvests, pier fishing culture in Los Angeles County was evident across the research loci. There is an established subsistence fishing culture on these piers and such cultures served as the foci "communities" for this project. The target piers were the Belmont Pier in Long Beach, the Redondo pier in Redondo Beach, Hermosa Beach Pier, and Cabrillo Beach Pier. Notably, the small-scale, consumptive fishing at the Cabrillo pier occurs in the shadow of the San Pedro area of Los Angeles, one of the major current and historical centers for commercial fishing in Southern California. In the port of San Pedro, commercial fisheries were valued at $19,444,000 in landing revenues alone (Norman, et al. 2007).

Theoretical and Analytical Framework

Subsistence fishing among non-indigenous populations in the United States has long been ignored as a significant coastal and aquatic activity. However, preliminary research has shown that small-scale fishing for individual dietary needs does occur nationwide (Jepson, et al. 2005). Knowledge regarding U.S. subsistence fishing remains shallow, however, due to both a paucity of research and the interpretation of the term *subsistence,* which in important institutions has been applied only to fishing as a primary source of

Fig. 1. Pier-fishing study sites in Los Angeles County.

food for a specific community (Schumann and Macinko 2007). Even for indigenous groups, subsistence hunting and fishing activities are sometimes called into question in the context of mixed economies or complicated sharing networks (Caulfield 1992). Ultimately, consistent and agreed-upon terminologies for describing local, non-commercial fisheries aimed not at recreation, but at individual and community consumption are lacking (Berkes 1998).

Prior seafood consumption studies in California and elsewhere have focused predominantly on demographics (Allen et al. 1006; APEN 1998; SFEI 2000), and at best have begun to introduce basic risk analyses (Connelley et al. 1996; Egeland and Middaugh 1997), leaving a gap between risk statistics and socio-cultural factors. While demographic data provide excellent baseline information, these data are often inadequate for defining what constitutes and defines these subsistence fishing communities, as well as their interest in subsistence fishing activities.

One of the suggested drivers for subsistence fishing is food insecurity, which is distinct from more extreme forms of hunger. Food insecurity is, in effect, a less visible status that is managed in inventive ways. Food insecurity coping practices include parents going hungry in order to transfer their meals to their children, or, for example, families repeatedly serving the same inexpensive foods. Food insecurity is overcome when families or individuals can maintain the "assured ability to acquire acceptable foods in socially acceptable ways (that is, without resorting to emergency food supplies, scavenging, stealing, or other coping strategies)" (USDA 2006).

Risks associated with inadequate food security involve not just shortages, but also the consumption of contaminated foods threatening human health. Fish resources are often promoted as the healthy dietary choice, the "brain food" rich in nutrients (Gomez-Pinilla

2008). Increasingly, however, health risks are included in statements about benefits. Fish consumption advisories are presented so that the subsistence or sport fisherman has to assess the risks of toxic exposure versus the benefits afforded in eating fish (Egeland and Middaugh 1997; Arnold et al 2005). In areas known to be at risk due to various forms of marine pollution, fishermen are often still present, their fishing activities undeterred. The oft cited reasons for ignoring warnings include distrust of the information provided in advisories and the assumption that larger closures would be enacted if the threats were serious (Burger and Gochfeld 1991; May and Burger 1996).

On the U.S. East Coast, in South Carolina, for example, education level, age, economic status, and ethnicity have all been found to correlate with the quantity of fish consumed (Burger et al 1999a). Ethnicity has also been found to affect how people receive information on fish consumption advisories and is related in general to their compliance with these warnings (Burger et al. 1999b). Along with Native American populations for whom wild caught fish consumption presents ceremonial, traditional and subsistence interests, Asian immigrant populations on the U.S. West Coast seem particularly at risk from consumptive, nearshore fishing (Sechena, et al. 1999).

Fisheries consumption studies to date have focused on toxicity risk through the consumption of sport-caught fish. Given the lack of socio-cultural data specific to this activity, however, it is important to determine the potential threat to human health posed by consumption of contaminated seafood, and to develop socio-culturally appropriate means for reducing exposure to toxins, while simultaneously discussing other drivers behind pier-caught fish consumption.

Results

Demographics, Food Security and Catch "Consumers"

Our set of demographic questions provided baseline information on survey respondents, including basic information about educational background, age, ethnicity and income levels of Los Angeles' pier-based fishers. Among those who indicated that they ate their wild catch, at least occasionally, 68% of the respondents answered that they had completed at least one year of college. While this descriptive measure reflected a somewhat surprising result in that we had posited little or no higher education experience for those we identified as catch "consumers," the fact is that our "consumer" survey respondents were defined as a much narrower group.

Catch "consumers" were identified as those survey respondents who consumed their pier-based catch at least 1–3 times or more in a two week period. These individuals were of particular interest to us in terms of environmental justice resource management policies, toxin exposure risks and data "gaps" in nearshore fishery management.

Research team members observed an array of ethnicities and languages on the four pier study sites. 43% of the respondents who claimed to eat the fish they caught identified their ethnicity as Spanish, Hispanic or Latino. Nevertheless, research team members observed a response bias which may have selected against Asian pier fishers. Asian pier-based fishers tended to decline to participate in the survey or were not proficient in English such that, absent a language-specific translator, research team members were not able to work with them in completing the survey. The Asian and Polynesian languages represented on the piers included Tongan, Samoan, Vietnamese, Tagalog and Chinese.

One important aspect of this survey was revealed in both the respondent comments and observations of pier fishers during our time in the field. Many of the pier-fishers typically had more than one fishing pole in the water per individual in the group, and subsequently

indicated that the quantity of catch was important to them. While most of the respondents indicated that they went fishing with friends, family members or both (60%), the goal of the outing was specifically to catch fish of a particular species meant for consumption. For example, 38% of survey respondents were specifically targeting halibut in their pier fishing efforts. Though it was then recommended that mackerel, for example, be consumed four times per month at most, the species was nevertheless targeted and eaten by 35% of those who consumed what they caught.

Slightly more than half of survey respondents identified "recreation" as the driver of their activities, as opposed to food or income. The 42% of research subjects who identified sustenance intentions over a recreational pursuit in their pier fishing activities were of particular interest to our research team. Indeed, 27% of all survey respondents indicated that they consumed their catch at least 1–3 times over a two-week period, placing one quarter of those surveyed in our catch "consumer" category.

Despite the fact that 77% of those respondents who ate the fish they caught claimed to make an annual salary of at least $50,000, 13% of these "higher income respondents" claimed that they sometimes or often did not have enough food to eat, indicating a possible discrepancy in the accuracy of reported income. This notion that income was inaccurately reported was posited again when our results demonstrated that 10% of these "higher income respondents" reported fishing mostly for food or income, and nearly one quarter said that they were fishing for both recreation *and* food or income.

Nevertheless, 23% of the catch "consumers" who indicated that they eat the fish they catch said that they depended on their self-caught marine resources as a cost-saving food source and as a dietary supplement. Another 31% suggested that they sometimes or often worried whether their food would run out before they had money to buy more, and 24% described not being able to eat balanced meals in the past year.

Pier Fishing and Risk Awareness

Our findings demonstrated that 85% of our survey respondents indicated a general awareness of the health warnings pertaining to the fish they caught. Despite the absence of written warnings as observed by the research team, many of the pier-based anglers were indeed aware of potential health risks through "word-of-mouth" and other means. Nevertheless, survey respondents disregarded these risks, and identified several reasons for doing so. The most prevalent reason given by respondents was that the printed material was simply not disseminated on a regular basis, and that their knowledge of the contamination levels of frequently caught fish was mainly distributed by "word of mouth," so it may have been arriving late into the formal identification and dissemination of a warning. Twenty-seven percent of the study participants responded that they consumed their catch at least one to three times over a two-week period, indicating that either they ignored the warnings or, that they were consuming the fish they caught as a cost-saving (23%) and/or supplemental dietary source (36%), regardless of warnings.

These data are important on several levels. First, despite obligatory efforts through the Montrose Settlements Restoration Program in collaboration with the United States Environmental Protection Agency to produce and disseminate printed material and to hold workshops regarding the risks of consuming pier-caught fish, the material is still not being presented to a large portion of the pier-based fishers in Los Angeles County. Additionally, pier fishers continue to target species that have high levels of contamination, including, for example, mackerel. These risk-oriented practices suggest that material communicating

consumption limits should be more widely available. Current permanent signage that exists at all four of the piers warns only of the harms associated with the consumption of white croaker (*Genyonemus lineatus*) and mussels (*Mytilus californianus*).

Pier Fishing, Food Security and Contaminant Risk

The majority of the pier fishermen with which we worked came from Los Angeles' immigrant populations. Immigrant populations of undocumented and unemployed adults constitute the highest risk for household food insecurity, and have not been part of an overall improvement in food security over the last several years (Harrison et al. 2007). Many of the Asian/Pacific Islander members of the pier fishing communities, despite precautionary measures taken by the U.S. Environmental Protection Agency (USEPA), as well as other locally oriented organizations, to warn against the danger of contaminated fish, were regularly seen fishing and preparing fish for consumption. These observations are in keeping with research from other areas of the U.S. West Coast (Sechena, et al. 1999). Our survey of these activities in Los Angeles County demonstrated that individuals from various ethnic groups do consume fish from LA County piers, as many as 27% of our respondents did so, despite problems with seafood contamination in the area.

While consumption of locally caught seafood by sport anglers may decrease issues of food insecurity, the practice nonetheless creates important issues related to potential toxin exposure. Fish consumption surveys have in fact revealed a threat to public health (West, et al. 1992; Allen, et al. 1996; SFEI 2000; Knuth, et al. 2003.) These studies have been carried out both in urban areas in California – Santa Monica Bay and San Francisco Bay (APEN 1998; SFEI 2000), as well as rural areas in the Great Lakes (West, et al. 1992), New York (Connelley, et al. 1996), King County, Washington (Sechena, et al. 1999; Sechena, et al. 2003), and at other sites.

Such studies have provided data relevant to the research presented here, in that they demonstrate which sub-populations are at the highest risk for contamination through consumption of pier-caught fish. For example, Asian anglers in the San Francisco Bay had the highest consumption rates, followed by African Americans and Latinos (APEN 2000). While these demographic data were and are important, an analysis of the underlying drivers for pier fishing activities was absent. In this research, we sought to compare our results to these prior research results while simultaneously examining the potential drivers for pier-based fishing. Our research furthered the notion that these contaminant risks were driven by issues of food insecurity at the pier fisher household level.

Part of the explanation for the risks associated with consuming pier-caught fish in the Los Angeles area are bound up in a history of local industries having discharged large amounts of dichlorodiphenyltrichloroethane (DDT) and polychlorinated biphenyls (PCBs) into the ocean off the Southern California coast. Discharge associated with industrial production occurred from the late 1940s to the early 1970s, and the majority of the DDT came from the Montrose Chemical Corporation's pesticide manufacturing plant in Torrance, California. The plant discharged waste into Los Angeles County Sanitation District sewers that empty into the Pacific Ocean at White Point, on the Palos Verdes shelf.

While the United States banned the use of DDT in 1973, and PCBs in 1977, these contaminants are nonetheless slow to break down due to their stable chemical structure, and remain in the marine environment, accumulating in plants and animals. The United

States Geological Survey conducted surveys in 1992 and 1993 and found more than 100 metric tons of DDT and 10 metric tons of PCBs that still remain in benthic sediments of the Palos Verdes Shelf (Lee 1994). The sediment contamination extends from Santa Monica Bay to the Los Angeles/Long Beach harbors.

As a result, many of the most commonly caught and consumed wild fish in the LA area have levels of DDT that have prompted the State of California to issue consumption advisories , and many of these species have levels of PCBs that present additional concerns in terms of human consumption. While there are currently eight species or species groups that fall under the California State advisory for consumption, our research revealed that the permanent signage posted on each of the four piers surveyed only indicate a consumption advisory for white croaker and, in the case of Redondo Beach pier, mussels. Warning materials are available online in a variety of languages. However, despite three months of a varied daylight research presence on four of the most frequented Los Angeles piers, research team members did not encounter written fishing warning materials, suggesting that the material was not reaching all possible pier-based anglers.

Discussion

Across California, families are finding it increasingly difficult to cope with economic stagnation and disruptions in the economy. California's high cost of living often forces families to make difficult budgetary decisions. The California Budget Project found that a family of four would need to earn about $72,000 annually to make ends meet, though only one half of California's workers earn this amount even with two full-time workers contributing to the household (California Budget Project 2007). This lack of financial stability puts 30 percent of low-income California adults in a category of being unable to put adequate food on the table on a consistent basis, a percentage that has been rising since 2001 (Harrison, et al. 2007).

Los Angeles County, in particular, has an estimated 777,000 low income adults reporting hunger or food insecurity, with an estimated 1,734,000 other people living in these households, meaning that California has a 30% rate of food insecurity (California Food Policy Advocates 2008). More than three-quarters of a million low-income adults in Los Angeles County live with hunger or make daily decisions about whether to eat or pay for other essential needs such as shelter or clothing, according to a UCLA Center for Health Policy Research Report (Harrison, et al. 2007).

By focusing on poor, minority and immigrant populations who may indeed be accessing nearshore fisheries to cope with food insecurity issues, this research was organized around two broad policy goals: expanding the examination of communities in fisheries management, and advancing potential "environmental justice" research in the intersecting realms of fishery dependence, management and marine resource toxin risk.

Through the course of this survey, we have identified several regional regulatory agencies that would benefit from the data collected, as well as further research on coastal subsistence fishers, including the California Regional Water Quality Control Board, which ranks accounting of subsistence fishing high on its list of priority issues, (Los Angeles County Department of Public Health 2007). Additionally the work presented here could inform the Environmental Protection Agency, an agency that recognizes subsistence fishing to be substantial enough to have a clause in the Palos Verdes Shelf Superfund Site document. This clause states that the Montrose Settlements Restoration Program must create "improved recreational and subsistence fishing opportunities to

offset the impairment of fishing caused by contamination present in sports fish caught off the coast of Southern California." For the 27% of pier fishing catch "consumers" identified earlier, their use of the adjacent piers for sustenance only amplifies the importance of this clause.

Conclusion

Our research represents an overview of the nature of, and the problems associated with, pier fishing in Los Angeles County. Our findings therefore provide an understanding of the socioeconomic characteristics of sport anglers' seafood consumption from areas known to contain species exposed to toxins. Data on pier-based fishing activities and their linkages with consumption and food security may be used to direct further toxicity studies and more importantly, to inform efforts by local, state and federal government agencies and non-governmental organizations to identify at-risk groups and further develop socio-culturally appropriate education and outreach strategies that targets these groups.

Because fisheries management in general can prove to be complex, information about the social and economic values and uses of these fisheries, even at - indeed particularly at - a scale as small as the pier-based subsistence fisher, is an important asset for fishery managers, pollution mitigation policymakers and the greater public interested in coastal natural resources and food insecurity "creep." In Los Angeles County and in other West Coast urban areas, the fixture of the pier-based fishermen is not merely an expression of a quaint pastime, but may in fact be an indicator of the salient and entangled issues of food security and nearshore and human health.

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Soil Organic Carbon Storage in Restored Salt Marshes in Huntington Beach, California

Jason K. Keller,* Kimberly K. Takagi, Morgan E. Brown, Kellie N. Stump, Chelsea G. Takahashi, Woojin Joo, Kimberlee L. Au, Caitlin C. Calhoun, Rajesh K. Chundu, Kanani Hokutan, Jessica M. Mosolf, and Kylle Roy

School of Earth and Environmental Sciences, Chapman University, Orange, CA

Abstract.—There is a growing interest in managing wetland restoration and conservation projects to maximize carbon sequestration. We measured soil organic carbon storage and methane flux from two southern California salt marshes which had been restored for 2 and 22 years. We hypothesized that organic carbon would accumulate following restoration and that methane flux would be negligible in both sites. While methane flux was minimal, soil organic carbon content was generally higher in the more recently restored site. Although there is a potential for carbon sequestration in salt marshes, tracking this process through time may be complicated by initial site conditions.

Introduction

As a result of anthropogenic activities, atmospheric concentrations of carbon dioxide ($[CO_2]$) have increased from pre-industrial levels of ~280 ppm to current levels exceeding 379 ppm (Forster et al. 2007), the highest values seen for at least the past 650,000 years (Jansen et al. 2007). This rise in atmospheric $[CO_2]$ has led to an acceleration of sea level rise as well as changes in ecosystem carbon cycling (Denman et al. 2007). Among the many options for mitigating these impacts is the capture and storage of atmospheric CO_2 in long-lived carbon pools (Metz et al. 2007).

Long-term carbon storage in ecosystems is possible through the accumulation of biomass or soil organic matter. Wetland ecosystems may be particularly well suited for carbon storage because a lack of oxygen in flooded or saturated soils imposes a fundamental constraint on microbial decomposition, frequently resulting in the accumulation of soil organic matter (Megonigal et al. 2004). Indeed, wetland ecosystems have accumulated ~500 Pg of carbon in their soils, approximately one-third of the total terrestrial soil carbon on a global scale (Bridgham et al. 2006).

There is thus a growing interest in linking the carbon storage potential of wetland ecosystems to ongoing management efforts through the sale of carbon credits on emerging carbon markets (e.g., Galatowitsch 2009; Hansen 2009). Given the continued loss of wetlands from the landscape (Dahl 2011) and the high cost of wetland mitigations (Environmental Law Institute 2007), the potential opportunity for wetland projects to become partially "self-funded" is an intriguing possibility. The prevalence of ecosystem-based biosequestration projects on existing, voluntary carbon markets (Galatowitsch 2009) further highlights the appeal of this approach. Presumably, carbon credits could be awarded to a number of project types, including: (i) wetland restoration or creation projects that result in an increase in soil carbon and (ii) wetland conservation projects

* Corresponding author: Jason Keller jkeller@chapman.edu

that result in the preservation of existing soil carbon pools. Crediting these project types implicitly assumes that carbon accumulates through time following restoration and that wetland degradation leads to a loss of soil carbon stocks. However, it should be noted that there are a number of policy and scientific uncertainties surrounding this approach (Galatowitsch 2009; Hansen 2009; Palmer and Filoso 2009; Crooks et al. 2010).

The potential to sequester carbon in vegetated coastal ecosystems (i.e., "blue carbon"), including salt marshes, is particularly appealing in this context for several reasons (Irving et al. 2011; Mcleod et al. 2011). First, salt marsh ecosystems must accrete new soil to keep pace with sea level rise (Mudd et al. 2009; Kirwan et al. 2010). This results in a continual increase in the volume of soil where organic carbon can be sequestered and buries existing soil at deeper depths where persistent anaerobic conditions limit further decomposition. In a recent review, Chmura et al. (2003) estimated a carbon sequestration rate of 210 g CO_2 m^{-2} y^{-1} for tidal saline wetlands including salt marshes, a per area value which is an order of magnitude higher than sequestration rates in northern peatland ecosystems. Second, the presence of sulfate in sea water is assumed to suppress methane (CH_4) production due to the dominance of competitively superior sulfate reducing microbes (Megonigal et al. 2004; Poffenbarger et al. 2011) in salt marsh ecosystems. This is critical because CH_4 is a potent greenhouse gas with 25-times the global warming potential of CO_2 (Forster et al. 2007), and has been shown to offset the decreased radiative forcing due to carbon sequestration in freshwater wetland environments (e.g., Bastviken et al. 2011). While it is generally assumed that CH_4 fluxes are negligible in salt marsh ecosystems, these fluxes have rarely been quantified (but see Chmura et al. 2011; Poffenbarger et al. 2011).

Here, we measure the soil organic carbon storage and CH_4 flux in two adjacent salt marshes in southern California which have been restored for 2 and 22 years. We hypothesized that (i) the soil organic carbon pool would be larger in the older restoration site and (ii) CH_4 fluxes would be minimal at both sites. This work provides an important baseline for evaluating the potential for carbon sequestration in similar ecosystems and is unique for salt marshes in Southern California, where soil carbon storage has not been as well studied as in other locations such as the East and Gulf Coasts and the San Francisco Bay region.

Methods

Site Description

The Huntington Beach Wetlands utilized in this study are located in northern Orange County, California (Figure 1). These sites are relics of a larger, approximately 3000-acre, marsh complex that historically existed at the mouth of the Santa Ana River but has decreased in size as a result of anthropogenic activities (Grossinger et al. 2011). By the mid-1940s, these systems had been isolated from tidal exchange due to channelization of the Santa Ana River and flood control measures associated with local development as well as the construction of the adjacent Pacific Coast Highway (Jones & Stokes Associates 1997).

The current restoration of the 25-acre Talbert Marsh began in 1988, following a short-term, temporary reconnection to tidal exchange in 1979. Tidal flow was fully restored to Talbert in February 1989 following the removal of a levee from an adjacent flood control channel (the site remains disconnected from the Santa Ana River mouth). In 1991, a new tidal outlet was constructed and the old channel was closed (Jones & Stokes Associates 1997).

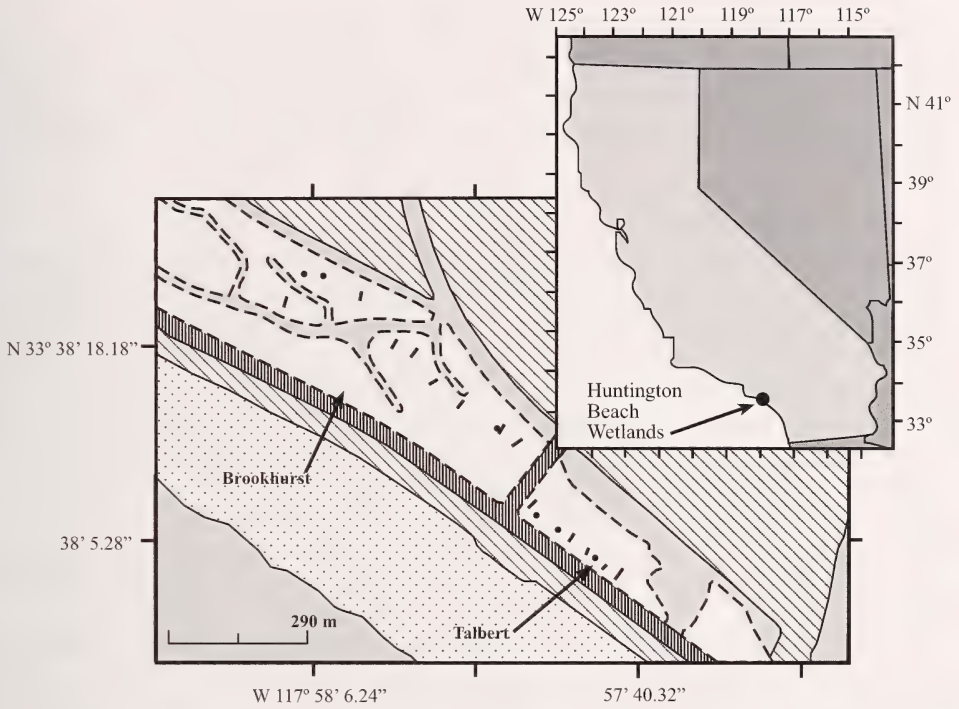

Fig. 1. Map of Talbert Marsh and Brookhurst Marsh in Huntington Beach, California. Talbert Marsh was restored in 1989 and Brookhust Marsh was restored in 2009. Marshes boundaries are indicated by dashed lines. Soil organic carbon was measured in 3 soil cores collected in each marsh (soil black circles). Net ecosystem respiration, including net CH_4 flux, was measured using 2 static chambers adjacent to each soil core. Belowground biomass was measured in 3 evenly-spaced root cores collected along existing vegetation monitoring transects (solid black lines) within each marsh.

Restoration of the adjacent, 67-acre Brookhurst Marsh began in 2008 and tidal flow was restored in July 2009 following the removal of a levee from the flood control channel (Gordon Smith, Huntington Beach Wetlands Conservancy, personal communication). Sites utilized for the current project were located in the mid/high marsh which is dominated by vegetation characteristic of southern California salt marsh ecosystems, including: *Sarcocornia pacifica* (Standl.) A.J. Scott (perennial pickleweed), *Frankenia salina* (Molina) I.M. Johnst (alkali seaheath), *Batis maritima* L. (saltwort), and *Distichlis spicata* (L.) Greene (saltgrass).

Soil Organic Carbon

To quantify soil organic carbon content, 3 soil cores were collected from both Talbert and Brookhurst Marshes in September-October of 2011 (Figure 1). Cores were collected to depths of ~42 cm (Talbert) and ~46 cm (Brookhurst) using a 15.3-cm diameter stainless steel tube equipped with a sharpened bottom edge. Despite the twisting and downward pressure required to collect soil cores, compaction of soils was minimal and depths to the soil surface measured from the inside and outside of the soil core were within 1.5 cm. Upon extraction from the core, soils were sliced into 2-cm depth increments using a serrated knife and returned to the laboratory at Chapman University for processing. Depth increments were dried to a constant mass at 60 °C for 2 weeks and then weighed to determine bulk density (g dry mass cm^{-3}). Subsamples of dried soils

from each depth were homogenized using a mortar and pestle and subsequently ground to a fine powder using coffee grinders. Organic matter content of ground soils was determined as loss on ignition (LOI) at 400 °C for 10 hours and converted to organic carbon content on a percent mass basis using the quadratic relationship described by Craft et al. (1991).

Net Ecosystem Respiration

Net ecosystem respiration (NER) was measured as the net flux of CO_2 and CH_4 using ~15 L dark, static chambers constructed from 29.8-cm diameter sewer PVC pipe. The bottom of the chambers had a sharpened, beveled edge and the top was routed and lined with a 2.4-mm diameter o-ring. NER was measured concomitantly with soil core collection using 2 chambers adjacent to each soil core (i.e., 6 flux measurements from each site). For each measurement, chambers were inserted to a depth of 2–3 cm below the soil surface and capped with a thick PVC cover equipped with a two-way stopcock to allow for gas sampling. Chamber covers were painted silver to minimize heating effects. Five headspace samples were collected at 10–15 min intervals using 10-mL syringes (also equipped with stopcocks). Samples were analyzed on the same day they were collected for CO_2 and CH_4 using a gas chromatograph equipped with a flame ionization detector and an in-line methanizer to convert CO_2 to CH_4 (SRI 8610C, SRI Instruments, Torrance, CA).

NER is expressed as μmol CO_2 m^{-2} min^{-1} based on the linear ($r^2>0.90$) accumulation of CO_2 over the measurement period. Because chambers enclosed intact vegetation, CO_2 produced was the combination of heterotrophic microbial respiration as well as autotrophic plant and algal respiration. Gas concentrations were corrected for the actual volume of the static chambers based upon measurements of the depth from the top of the chamber to the soil surface and for air temperatures obtained from a nearby weather station (http://www.wunderground.com/weatherstation/WXDailyHistory.asp?ID=KCAHUNTI3). Two chambers from Talbert and one chamber from Brookhurst which did not exhibit a linear accumulation of CO_2 (suggesting a faulty chamber seal) were excluded from subsequent analysis. We did not observe linear accumulation (or decline) of CH_4 in any chamber.

Belowground Biomass

Belowground biomass was measured using root cores collected using 5.08-cm diameter aluminum cores to a depth of 20 cm. Cores were collected along transects previously established for monitoring vegetation cover in both sites (Christine Whitcraft et al., California State University, Long Beach, unpublished data). There were 5 transects in the mid/high marsh in Talbert and 9 in Brookhurst. Soil cores used to measure organic carbon content were bracketed by at least 2 adjacent transects (Figure 1). Root cores were stored at 4 °C for up to 10 d prior to analysis. Cores were subsequently washed over a 1 mm soil sieve and living roots were collected and dried at 60 °C for 48 h. Additionally, two belowground biomass cores were taken adjacent (within 2 m) to each of the soil cores. Belowground biomass was expressed as kg dry biomass per m^3 soil volume.

Statistical Analysis

Differences in soil organic carbon content between Talbert and Brookhurst were analyzed using a repeated measures ANOVA with depth as a repeated, within-subject factor and site as a fixed, between-subject factor. Across all depths, soil organic carbon content data were not normally distributed even following common transformations

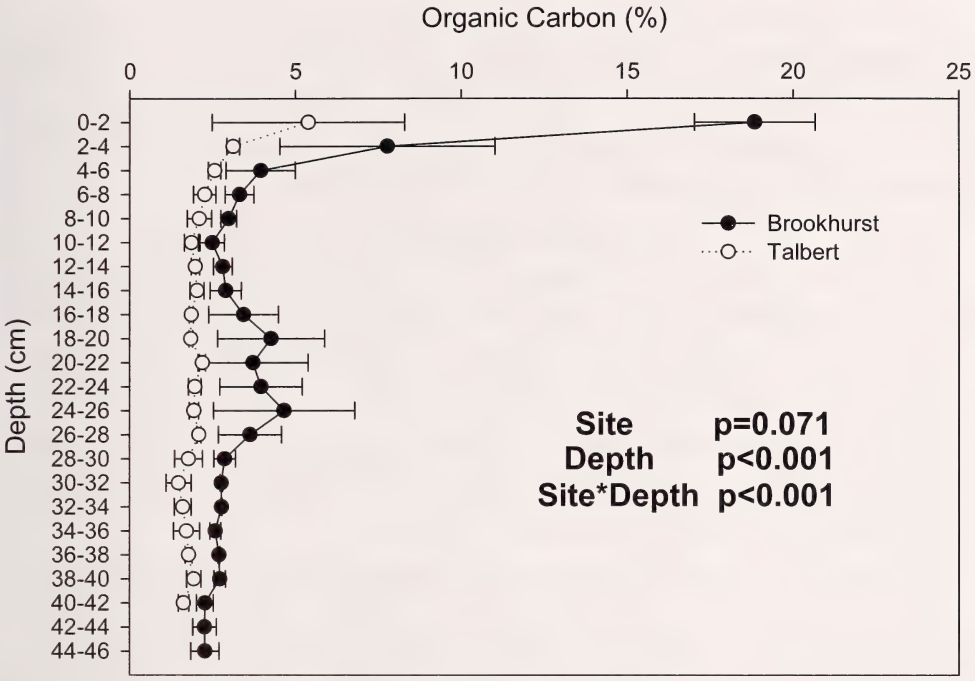

Fig. 2. Depth profiles of soil organic carbon content (mean ± 1 SE) in Talbert (restored in 1989) and Brookhurst (restored in 2009) Marshes. Results of a repeated measures ANOVA with site as a fixed factor and depth as a repeated factor are shown.

(e.g., arcsin square root and logarithmic transformations). The repeated measures ANOVA was performed on un-transformed data. We used t-tests to analyze differences in NER, belowground biomass, and total carbon storage between Talbert and Brookhurst. Belowground biomass data were logged-transformed to meet assumptions of normality prior to analysis. Linear regressions were used to explore potential relationships between belowground biomass (collected adjacent to soil cores) and cumulative soil carbon storage in the upper 10 and 40 cm of the soil profile. All analyses were completed using PASW Statistics 18 (SPSS 2009).

Results

Mean percent soil organic carbon was higher at all depths in the more recently restored Brookhurst Marsh than in Talbert Marsh (Figure 2). However, differences between sites varied by depth (depth * site interaction $F(20,80)=6.338$, $p<0.001$; Figure 2). In both sites, the highest organic carbon content was seen in the surface 0–2 cm with 18.8 ± 1.8% and 5.4 ± 2.9% (mean ± 1 SE) in Brookhurst and Talbert, respectively. When corrected for bulk density, the total amount of organic carbon held in the upper 40 cm of the soil profile (mean ± 1 SE) did not differ between sites with 13.6 ± 0.3 kg carbon m^{-2} in Brookhurst and 9.3 ± 0.8 kg carbon m^{-2} in Talbert ($t(4)=1.58$, $p=0.19$).

NER as net CO_2 flux was similar between sites ($t(7)=0.18$, $p=0.87$) with values (mean ± 1 SE) of 113.5 ± 23.3 μmol CO_2 m^{-2} min^{-1} and 106.7 ± 32.2 μmol CO_2 m^{-2} min^{-1} in Brookhurst and Talbert, respectively. Given the lack of CH_4 accumulation in the chambers, net CH_4 flux was assumed to be negligible at both sites.

Belowground biomass (mean ± 1 SE) based on root cores to a depth of 20 cm was 7.0 ± 1.2 kg dry biomass m^{-3} in Brookhurst and 9.4 ± 3.2 kg dry biomass m^{-3} in Talbert, and did not differ between sites ($t(40)=0.25$, $p=0.81$). Across both sites, there were no relationships between belowground biomass (from root cores collected adjacent to the soil cores) and cumulative soil organic carbon storage in the upper 10-cm of the soil profile ($p=0.51$) or the upper 40-cm of the soil profile ($p=0.64$).

Discussion and Conclusions

Both Talbert and Brookhurst Marshes stored organic carbon in their soils. When averaged across all depths to 40 cm, organic carbon densities (± 1 SE) were 0.034 ± 0.006 and 0.023 ± 0.002 g cm^{-3} in Brookhurst and Talbert, respectively. These values are comparable to the 0.039 ± 0.003 g cm^{-3} soil carbon density of salt marsh soils reported by Chmura et al. (2003). Of the sites used by Chmura et al. to calculate this average, only 6 were from the Northeastern Pacific, including 3 data points from a single southern California marsh complex in Tijuana Slough, California (Chmura et al. 2003). The average soil carbon density from the Tijuana Slough site was 0.025 ± 0.008 g cm^{-3} which is comparable to the values measured in the current study.

In contrast to our initial hypothesis, mean percent organic carbon was higher at all depths in the more recently restored Brookhurst Marsh, although the magnitude of these differences depended on soil depth (Figure 2). This apparent lack of carbon accumulation through time differs from a number of studies which have shown that soil organic carbon content frequently increases following wetland restoration activities (e.g., Craft et al. 2003; Cornell et al. 2007). However, a recent meta-analysis suggests that soil carbon pools recover slowly following wetland restoration, and are generally well below values seen in reference marshes even many decades following restoration (Moreno-Mateos et al. 2012).

Streever (2000) cautioned against drawing too strong a conclusion from chronosequence approaches because the magnitude of inter-site differences in ecosystem properties are often greater than changes in those properties observed through time. We hypothesize that this was the case in the Huntington Beach wetlands used in this study, and that differences in soil organic carbon content were driven by initial site conditions in Talbert and Brookhurst, rather than by processes occurring during the additional 20 years of post-restoration development at Talbert. Pre-restoration vegetation surveys along 2 transects in Talbert Marsh suggest that total vegetation cover was less than 40% (Jones & Stokes Associates 1997), much lower than pre-restoration cover values of 88% measured along the 9 transects used to measure belowground biomass in Brookhurst Marsh (Christine Whitcraft et al., unpublished data). The lack of differences in standing belowground biomass and NER between sites despite a 20-year difference in age also suggests that carbon cycling may be similar at both sites despite their different ages.

Further, Maezumi (2010) collected a single core from Brookhurst prior to marsh restoration in 2008 and observed organic carbon content of ~9% in the surface 0–1 cm compared to a value of ~7% in the surface soil of a single core collected from Talbert in the same year. These values differ from the average organic carbon contents measured in our study (~19% and ~5% in the surface 2 cm for Brookhurst and Talbert, respectively); however, they suggest that higher organic carbon content in Brookhurst soil may have existed prior to restoration of this site. This highlights the importance of collecting baseline, pre-restoration data if increased carbon sequestration is a goal of wetland management activities. The presence of elevated soil organic carbon in Brookhurst despite being disconnected from tidal influence for nearly a century may also call into

question the assumption that soil carbon is rapidly lost following the introduction of aerobic soil conditions in wetland environments, and may have important implications for wetland conservation projects that hope to capitalize on maintaining existing soil carbon pools.

Our NER measurements suggest that net CH_4 flux was not significant during our samplings. The lack of significant CH_4 fluxes from this salt marsh site is consistent with the limited previous work on this topic. Poffenbarger et al. (2011) suggest that at soil salinities above 18 ppt, which are common at Brookhurst and Talbert, CH_4 flux is minimal due to competitive suppression by sulfate reducing microbial activities. Chmura et al. (2011) also demonstrated that small, but measurable, end of season fluxes of the greenhouse gases CH_4 and nitrous oxide (N_2O) did not offset CO_2 uptake and storage in Canadian salt marshes. While our data support the assertion that salt marshes may be ideal sites for carbon sequestration due to a lack of substantial CH_4 fluxes, we cannot rule out the possibility of measurable CH_4 fluxes from more brackish portions of these sites or following major rain events which can bring large amounts of freshwater into these systems. Previous work on soils from salt marshes in southern California demonstrates that CH_4 production is possible in anaerobic laboratory incubations within a few days (Jason Keller, unpublished data) suggesting a potential for this metabolic process in these soils.

Storage of organic carbon through the soil profile and a lack of CH_4 fluxes in two restored southern California salt marshes reinforce the potential for these systems to be managed to maximize carbon sequestration. Soil organic carbon content in these systems is comparable to marshes in other, better-studied, geographical regions. However, higher soil carbon content in the more recently restored Brookhurst Marsh demonstrate that soil organic carbon may persist even in the absence of tidal connectivity in these systems and highlight the importance of initial site conditions in tracking soil carbon storage in restoration projects. A lack of significant CH_4 fluxes from both sites is consistent with previous research; however, additional work is necessary to quantify potential spatial and temporal variability in this important process.

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